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New Middle Eocene Omomyines (Primates, Haplorhini) from the Friars Formation of San Diego County, Southern California

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New Middle Eocene Omomyines (Primates, Haplorhini) from the Friars Formation of San Diego County, Southern California

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Dedication

This thesis is dedicated to Stephen L. Walsh, who worked in the Department of Paleontology at the San Diego Natural History Museum from 1988 until his untimely death in August of 2007. His passion and dedication to paleontology, biostratigraphy, and biochronology made this thesis possible, and his work has been greatly appreciated by the author.

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Abstract

New Middle Eocene Omomyines (Primates, Haplorhini) from the Friars Formation of San Diego County, Southern California

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The Friars, Mission Valley, Santiago, and Sespe formations in Southern California are composed of fluvial sediments and represent the Uintan North American Land Mammal Age. The omomyoid primates currently recognized from the Uintan of San Diego County include *Dyseolemur*, *Chumashius*, *Hemiacodon*, *Washakius*, *Macrotarsius, Stockia, Yaquius,* and *Ourayia*. Here we describe three new genera of Middle Eocene primates from the Friars Formation of San Diego County. Thirty-two teeth represent *Ekwiiyemakius*. *Ekwiiyemakius* is the smallest of the new taxa and has an estimated body mass of 119 g. This new genus is distinguished by a discontinuous lingual cingulum and a waisted distal margin on the upper molars. Sixty-four specimens represent *Cabrillotarsius*. At 289 g estimated body mass, *Cabrillotarsius* is intermediate in size. *Cabrillotarsius* has a distinctive upper fourth premolar with a mesio-buccally oriented protocone and upper molars with a strong, lingually continuous cingulum. A sample of thirty-nine teeth and mandibular fragments represent a third new genus, *Brontomomys*. With an estimated body mass of 757 g, this large omomyine is similar in

size to *Macrotarsius jepseni*. However, *Brontomomys* is distinct from other large omomyines in having a small p4 paraconid and large m2-m3 paraconids that are twinned with the metaconid. The results of phylogenetic analyses vary according to (1) the choice of character-taxon matrix and (2) the use of parsimony versus Bayesian tree building methods. Nevertheless, all preliminary phylogenetic analyses are congruent in recovering a close relationship between the three new San Diego taxa and the omomyines *Ourayia*, *Macrotarsius*, *Utahia*, and *Omomys*. Prior research has documented a shift in omomyoid diversity in North America from the anantomophine-rich Bridgerian to the omomyine-rich Uintan. Our description of three new Uintan omomyine taxa further emphasizes these opposite trends in anaptomorphine and omomyine species richness during the Middle Eocene. All of the new taxa are currently only known from the Friars Formation in San Diego County, California. Four of the previously known genera from San Diego County (*Dyseolemur, Chumashius, Yaquius,* and *Stockia*) are endemic to Southern California, further highlighting the provincial character of primate faunas in Utah, Southern California, and West Texas during the Uintan.

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INTRODUCTION

The Middle Eocene strata of San Diego County are composed of mammal-bearing fluvial units interfingering with fossiliferous marine deposits (Figure 2). This paper will focus on one formation from San Diego County: the Friars Formation. The Friars Formation of Southern California is composed of fluvial conglomerates interfingering with lagoonal mudstones, which have been correlated with the Middle Eocene based on biostratigraphy and magnetostratigraphy (Figure 2; Walsh et al., 1996). Early work on the mammalian fauna of the Friars Formation firmly placed this unit within the Uintan (Walsh, 1987), but little research has been undertaken on the primates of the Friars Formation since Lillegraven's seminal publication in 1980. Lillegraven (1980) identified three omomyoids from the Friars Formation: *Omomys powayensis*, ?*Macrotarsius* sp. near *M. jepseni*, and *Washakius woodringi*. While Lillegraven did not recognize *Stockia powayensis* as legitimate in 1980, other researchers have continued to treat *Stockia* as a valid genus. Walsh (1996) does not recognize Lillegraven's *Omomys powayensis* nor ?*Macrotarsius* sp. near *M. jepseni,* but hints at new species of both *Omomys* and *Ourayia* from the Friars Formation. Unfortunately, Walsh did not formally describe these new taxa. Many of the SDNHM specimens described in this paper were originally catalogued by Walsh in the early 1990s, and labeled "*Ourayia* sp. nov and *Omomys* sp. nov., which supports the notion that he provisionally allocated these new specimens from the Friars Formation to known genera. After 1980, no additional formal work was done on the Friars Formation omomyoids. Since then, other paleontological studies of omomyoids from Southern California have focused on the younger Sespe Formation and the endemic *Yaquius travisi* (See Table 1; Mason, 1990).

This paper seeks to augment our understanding of Uintan primate faunas from Southern California by documenting the existence of three new genera of omomyoid primates from the Friars Formation. These specimens were collected by field crews from the San Diego Museum of Natural History during the 1980s and 1990s, but have not been formally described until now. We also aim to gain a better understanding of the evolutionary relationships between the new taxa described, and already published Uintan omomyoids from lower latitudes. We also discuss the implications of this research for North American patterns of species richness during the middle Eocene.

Primates initially flourished in North America during the early Eocene, marked by the arrival of *Teilhardina* approximately fifty-six million years ago (Szalay, 1976; Savage and Russell, 1977; Szalay and Delson, 1980; Gingerich, 1981; Rose and Bown, 1991; Smith et al., 2006). This immigration event was likely driven by high global temperatures brought on during the Paleocene-Eocene Thermal Maximum and Early Eocene Climatic Optimum (Smith et al., 2006). Primates diversified rapidly in North America during the Early Eocene, specifically, the anaptomorphine omomyoids experienced high species richness during the Bridgerian Land Mammal Age (Robinson et al., 2004; Gunnell et al., 2009). The high diversity of anaptomorphine primates includes taxa such as *Tetonius, Shoshonius, Hemiacodon*, and *Anemorhysis* (Bown and Rose, 1984; Honey, 1990).

After the Early Eocene, however, primate diversity in North America began to shift. During the Uintan, omomyine primates such as *Diablomomys, Ourayia, Macrotarsius, Chumashius*, and *Yaquius* slowly replaced the anaptomorphine-rich ecosystems that dominated the Bridgerian (Lillegraven, 1980; Szalay and Delson, 1980; Mason, 1990; Williams and Kirk, 2008). In large sections of the Rocky Mountain interior primates disappeared completely (Gunnell, 1995; Gunnell and Bartels, 1999; Williams and Kirk, 2008). During the Middle and Late Eocene there are limited strata in North

America that preserve primate fossils, as the fauna of Colorado and Wyoming all experienced primate extinction by the Late Eocene (Gingerich, 1981; Gunnell and Bartels, 1999). The Eocene strata of San Diego County, however, records primate evolution spanning the Middle and Late Eocene (Figure 1). The early Uintan is represented in San Diego County by the vertebrate-bearing Scripps and Friars Formations and the overlying Stadium Conglomerate (Kennedy and Moore, 1971). The fauna from the Scripps, Friars, and Stadium Conglomerate comprise the Poway fauna (Walsh, 1996). The Mission Valley Formation and the Pomerado Conglomerate represent the late Uintan (Walsh, 1996; Walsh et al., 1996). The Uintan strata of San Diego County, California, thus provide one of the only windows into the evolution of North American primates during this period of faunal turnover.

The Friars Formation is of particular importance as it has largely yielded a mammalian fauna similar to that seen in the middle Eocene of Wyoming and Utah, such as the presence of *Notharctus* and *Hemiacodon* (Walsh, 1996). It is interesting to note that these taxa are abundant in the Rockies during the Bridgerian, and only persist into the Uintan at lower latitudes (Golz and Lillegraven, 1977; Lillegraven, 1980; Walsh, 1996). The later occurring fauna found within the Mission Valley Formation and the Pomerado Conglomerate are, in contrast, highly endemic (Golz and Lillegraven, 1977; Lillegraven, 1980; Walsh, 1996). This faunal transition from well-distributed taxa found across North America to highly regionalized communities is another reason why studying the Friars Formation is crucial.

Geology of the Friars Formation

During the Middle Eocene the coastal plain of San Diego County, California, experienced deposition of both mammal-bearing fluvial strata containing fauna from the Uintan North American Land Mammal Age (NALMA) as well as fossiliferous marine deposits (Kennedy and Moore, 1971; Walsh et al., 1996). These Eocene geologic units make up the La Jolla Group and the Poway Group of San Diego County, California, which lie unconformably on the Upper Cretaceous Rosario Group (Figure 2). This depositional environment is significant as it is one of the only places in North America that offers direct correlation of the Bridgerian and early Uintan NALMAs with various marine index fossils (Westgate, 1988; Walsh et al., 1996; Robinson et al., 2004).

While the Eocene rocks of San Diego County are relatively undeformed, interpreting their depositional histories has proven to be challenging. This obstacle is likely from the rapid lateral facies changes and confusing disconformities along a quickly changing coastline, similarities in sedimentary lithologies, a lack of naturally occurring outcrops, removal of Eocene strata by Plio-Pleistocene erosion, and significant local faulting (Peterson and Kennedy, 1974; Walsh et al., 1996). Kennedy and Moore (1971) and Kennedy and Peterson (1975) divided the Middle Eocene strata from San Diego County in the marine-dominated La Jolla Group (Mount Soledad Formation, Delmar Formation, Torrey Sandstone, Ardath Shale, Scripps Formation, and Friars Formation) and the overlying, largely nonmarine Poway Group (Stadium Conglomerate, Mission Valley Formation, and Pomerado Conglomerate). Their model assumed continuous deposition during the middle Eocene times. Three gradual marine transgressions and three gradual marine regressions were invoked by Kennedy and others to explain the lateral facies changes (Kennedy and Moore, 1971; Kennedy and Peterson, 1975).

Walsh, Prothero, and Lundquist (1996) question the ages of the deposits identified by Kennedy and workers, and revised the stratigraphy of the upper Cretaceous and Eocene units in southwest San Diego County. Their interpretation is still largely based on the transgressive-regressive model of Kennedy and Moore, but with key differences. These differences include acknowledging a Wasatchian age formation between the Upper Cretaceous Cabrillo Formation and the Middle Eocene (Bridgerian NALMA) Mount Soledad Formation (Walsh, 1991), and stratigraphically expanding the Friars Formation (Walsh et al., 1996). The Friars Formation is now recognized as having three tongues: a lower sandstone-mudstone tongue, a middle conglomerate tongue, and an upper sandstone-mudstone tongue.

The Friars Formation was named by Kennedy and Moore (1971) for the vertebrate-bearing fluvial sandstones, siltstones, and mudstones that occur above the marine sandstones and siltstones of the Scripps Formation, and below the conglomerates of the fluvial Stadium Conglomerate (Walsh et al., 1996). The lower tongue of the Friars Formation consists mostly of sandstones and mudstones, and is fluvial origin in the east, and partly lagoonal origin in the west. The middle conglomerate tongue erosionally overlies the lower tongue and in the east is fluvial in origin, and in the west is deltaic in origin. The uppermost tongue consists of sandstone and mudstone, and like the lower tongue is fluvial in origin to the east, and lagoonal in origin to the west. All three units of the Friars Formation have produced early Uintan mammal fauna (Ui1), marked by the presence of *Leptoreodon major* and other selenodont artiodactyls, and are collectively referred to as the Poway fauna (Walsh, 1996; Robinson et al., 2004).

In 1986 Flynn integrated paleomagnetic data with mammalian biochronology in order to correlate the early Uintan units and faunas of San Diego with those of Wyoming (Walsh et al., 1996). Flynn (1986) correlated the normal polarity interval in the Scripps

and basal Friars Formations with Chron C21n, and the reversed polarity interval in the upper part of the Friars Formation with Chron C20r. Bottjer et al. (1991) agreed with Flynn (1986) and reported that sites from the base of the Friars Formation were of normal polarity and correlated with Chron C21n. These correlations firmly place the Friars Formation in the middle Eocene, approximately 46 to 44 Ma. These dates line up with the beginning of the Uintan, which is currently considered to have begun 46.2 Ma and ended 42 Ma (Gunnell et al., 2009; Kelly et al., 2015).

Walsh et al., (1996) found that the type area for the Friars Formation is very straightforward: the lowermost section of the Friars Formation is of normal polarity, while the upper section is reversed (Flynn, 1986; Bottjer et al., 1991). The magnetostratigraphic interpretations for the Friars Fm become more challenging to the north and east of the type section, where the formation is divided into the three subunits, such that the upper and lower sandstone/mudstone tongues are separated by the middle conglomerate tongue. Discrepancies are recorded in the conglomerate and upper tongues, where both normal and reversed polarities are found at different sites (Walsh et al., 1996). The most parsimonious reason for this variation in magnetostratigraphic signals of the Friars Fm is likely lithostratigraphic time-transgression, meaning the deposition of these units preserved in one area began earlier than the deposition of that same rock unit preserved in other areas (Kennedy et al., 1975; Walsh et al., 1996).

There have been no published studies on the absolute age of the Friars Formation. While the majority of dating techniques have been based on biostratigraphy and magnetostratigraphy, the younger Mission Valley Formation has yielded an Ar/Ar date of 42.83 +/- 0.24 Ma (Walsh, 1996). The Mission Valley Fm and the underlying upper Stadium Conglomerate have faunal assemblages distinct from that of the Friars Formation, late Uintan (Ui2-3) in age (Walsh et al., 1996).

MATERIALS AND METHODS

The fossils of *Ekwiiyemakius*, *Cabrillotarsius*, and *Brontomomys* described here are housed in the collections of the San Diego Natural History Museum (SDNHM; San Diego, California, United States). The comparisons made to other taxa in this paper are based primarily on the examination of epoxy resin casts of fossils from other North American localities, with the exception of *Diablomomys dalquesti*. Published photographs and drawings were used to supplement the comparisons (Gazin, 1958; Szalay, 1976; Beard, 1987; Mason, 1990; Williams and Kirk, 2008). Nomenclature used for dental morphology follows that of Ni et al. (2016) and is illustrated in Figure 3. Upper teeth are designated by uppercase letters, and lower teeth are designated by lowercase letters.

Specimens were measured to the nearest 0.01 mm using Mitutoyo digital calipers. Additionally, all specimens were digitally photographed with a scale bar using a Leica M80 Microscope equipped with a Leica IC80 HD camera. In case teeth were in situ in either the mandible or maxilla, measurements were taken from digital photographs using the line segment and measure tools in ImageJ (Schneider et al., 2012). Body mass was estimated using the all primate and prosimian least-squares regression equations presented in Conroy (1987). The equations are:

All Primate $\ln(B) = 1.784 \ln(A) + 2.54$ with a standard error range of +/- 0.33

Prosimian $\ln(B) = 1.614 \ln(A) + 2.67$ with a standard error range of +/-0.22

In the equations, B is body mass in grams and A is the area of the m1 in millimeters. The m1 area is calculated as the product of tooth crown length and width (Conroy, 1987; Kirk and Simons, 2001).

CT Scans

Twenty-four specimens were selected for computer tomography (CT) scanning at the University of Texas High-Resolution X-ray Computed Tomography Facility. We scanned two mandibular specimens attributed to *Brontomomys*, SDNHM 55253 and SDNHM 55252, during one scan of the North Star Imaging (NSI) scanner. The NSI scan uses a Fein Focus High Power source, which resulted in 8-bit imagery at 15.2 micron voxel resolution. Seven specimens of *Ekwiiyemakius* (SDNHM 96637, SDNHM 39750, SDNHM 55168, SDNHM 141153, SDNHM31649, SDNHM 39756, SDNHM 39758), Six specimens of *Cabrillotarsius* (SDNHM 38126, SDNHM 55250, SDNHM 56991, SDNHM 87871, SDNHM 46439, SDNHM 43094), and nine specimens of *Brontomomys* (SDNHM 60683, SDNHM 105007, SDNHM 60681, SDNHM 58005, SDNHM 55819, SDNHM 60684, SDNHM 60671, SDNHM 56700, SDNHM 58008) were scanned with the Xradia microXCT scanner resulting in 16-bit imagery with voxel resolution at 7.34 microns. VGStudio 3.0 was used for image processing.

Phylogenetic Analysis

The phylogenetic analyses were based on two different character-taxon matrices: Ni et al. (2016) and Tornow (2008). The Ni et al. (2016) matrix includes 1890 characters scored for 196 taxa.

Here we pared the Ni et al. (2016) matrix to include only 510 dental characters. We limited the taxa included to North American omomoyids (n = 25 genera) and Eurasian taxa (n = 10 genera). The Eurasian primates included are *Teilhardina asiatica*, *T. belgica*, *T. branti, T. magnoliana, Pseudoloris parvulus, Nannopithex zuccolae, Necrolemur spp., Microchoerus erinaceus, Donrussellia gallica and D. provincialis*. We

then added character scorings for the three new omomyoid genera described in this paper, as well as four additional North American genera that were not included in the Ni et al. (2016) matrix: *Yaquius travisi, Stockia powayensis, Diablomomys dalquesti*, and *Utahia kayi*. Editing of the Ni et al. (2016) character-taxon matrix and generation of the final NEXUS file for analysis was undertaken in Mesquite v3.2 (Maddison and Maddison, 2017).

The Tornow (2008) matrix included 100 characters, including 76 dental and 24 cranial and postcranial characters. The Tornow matrix includes 25 North American omomyoid taxa. We then added character scorings for the three new omomyoid genera described in this paper. Editing of the Tornow (2008) character-taxon matrix and generation of the final NEXUS file for phylogenetic analysis was accomplished in Mesquite v3.2 (Maddison and Maddison, 2017).

Parsimony analysis of the two resulting character-taxon matrices (hereafter referred to as the "Ni" and "Tornow" matrices) was undertaken using PAUP* (Swofford, 2003). For each matrix, we ran a heuristic search under the parsimony criterion with 100000 random addition sequence replicates, with random starting trees, and swapping using TBR. We then applied the bootstrap resampling method to the resulting majority-rule consensus tree. The bootstrap analysis consisted of generating 1000 pseudoreplicate trees. For each pseudoreplicate tree, PAUP* performed a heuristic search and retained all groups in the majority-rule consensus tree, including those with less than 50% support. All characters were assigned equal weight. Outgroups selected for parsimony analyses included *Teilhardina asiatica* for the Ni matrix, and *Teilhardina americana* for the Tornow matrix.

Additionally, Bayesian phylogenetic analyses of the Ni and Tornow matrices were undertaken using MrBayes v3.2.6 (Ronquist et al., 2012). The most widely used

model for estimating phylogenetic trees from discrete phenotypic data is the Mk model proposed by Lewis (Lewis, 2001; Wright and Hillis, 2014). This Mk models assumes a Markov process for character change, which allows for multiple character-state changes along a single branch (Wright and Hillis, 2014). For our analyses, MrBayes used the Mk model with the Dirichlet distribution parameter fixed to 1.0, which allows for a uniform prior on the proportions of the state frequencies (Ronquist et al., 2005). A gamma-distributed rate model, a random start tree, and a consensus tree output were selected. The Ni matrix ran for 3500000 mcmc generations, with a sample frequency of 500 in order to maximize sampling from the posterior probability. The Ni matrix analysis used two chains with a temperature of 0.025. *Teilhardina asiatica* was selected as the outgroup for the Bayesian analysis of the Ni matrix. The Tornow data matrix ran for 2000000 mcmc generations, with a sample frequency of 500. The number of chains was set to two, and the chain temperature equals 0.017. *Teilhardina americana* was chosen as the outgroup for the Bayesian analysis of the Tornow matrix.

RESULTS

Body Size

Figures 4-13 depict the length and width dimensions of the upper and lower dentition of *Ekwiiyemakius*, *Cabrillotarsius*, and *Brontomomys*. The body size estimates for the new taxa covered are in Table 2. The prosimian regression equation estimated *Ekwiiyemakius* to have a mass of 119 g with a 95% confidence range of 113 – 125 g. The all primate regression estimated *Ekwiiyemakius* to have a mass of 131 g and a 95% confidence range of 124 – 138 g. The prosimian regression equation estimated *Cabrillotarsius* to have a mass of 289 g with a 95% confidence range of 275 – 303 g. The all primate regression estimated *Cabrillotarsius* to have a mass of 348 g and a 95% confidence range of 330 – 366 g. The prosimian regression equation estimated *Brontomomys* to have a mass of 757 g with a 95% confidence range of 719 – 796 g. The all primate regression estimated *Brontomomys* to have a mass of 1008 g and a 95% confidence range of 958 – 1061 g.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758

Semiorder HAPLORHINI Pocock, 1918

Suborder OMOMYIFORMES Trouessart, 1879

Family OMOMYIDAE Trouessart, 1879

Subfamily OMOMYINAE Trouessart, 1879

EKWIIYEMAKIUS, gen. nov.

Type species. *Ekwiiyemakius walshi*

Generic diagnosis. Omomyine primate that differs from other North American omomyiforms except *Omomys, Macrotarsius, Diablomomys, Chumashius*, and *Rooneyia* in lacking a postprotocone fold on the upper first molar. Differs from all other North American omomyiforms except *Washakius* and *Rooneyia viejaensis* in the presence of a deep sulcus between the protocone and hypocone of the M1-2 (Figure 22). Length and width measurements of the upper and lower dentition are absolutely smaller than *Omomys, Yaquius, Stockia, Macrotarsius*, and *Ourayia*, similar in size to *Washakius woodringi,* and *Dyseolemur,* and larger than *Utahia* (see Table 3). Differs from *Omomys* in having an M1 that lacks a pericone, having a discontinuous lingual cingulum, and in having larger conules. Further differs from *Omomys* in having a more waisted distal margin of M1-2, and in lacking a lingual cingulid on the p3-4. Differs from *Stockia* and *Utahia* in having a lingually positioned m2 paraconid that is lower in height relative to the metaconid, in having lower molar trigonids that are less mesio-distally constricted, and in having m2-3 molar trigonids that are more open lingually. Further differs from *Stockia* in having a well developed p4 metaconid. Differs from *Yaquius* in having a p3 that lacks a buccal or mesiobuccal cingulid, and in having a relatively mesiodistally

longer p4 with a cuspate paraconid. Further differs from *Yaquius* in having an m1 paraconid that is buccolingually positioned between the protoconid and metaconid. Differs from *Diablomomys* in the presence of the postmetaconule crista on M1-2, in having a larger M1 hypocone, and in having an M2 with a waisted distal margin. Also differs from *Diablomomys* in having a p4 with a mesiodistal length similar to that of the m1 and a p4 metaconid height that is much lower relative to the height of the protoconid. Differs from *Macrotarsius* and *Ourayia* in lacking crenulated enamel and in having upper molars that lack a mesostyle and exhibit weakly developed distal and mesial cingula. Differs from *Washakius* in lacking crenulated enamel, and in having a smaller paraconule and metaconule.

Etymology. Derived from the Kumeyaay place name 'Ekwiiyemak' ("behind the clouds") for the Cuyamaca region of eastern San Diego County.

EKWIIYEMAKIUS WALSHI, sp. nov. (Fig. 18)

Holotype. Specimen SDNHM 96639, isolated M1.

Paratypes. Specimen SDNHM 96637, isolated p4; SDNHM 39750, isolated m1; SDNHM 55168, isolated m2; SDNHM 141153, isolated m3; SDNHM 39756, isolated M2, SDNHM 39758, isolated M3.

Hypodigm. p4: SDNHM 5511, SDNHM 105007, SDNHM 46365; m1: SDNHM 96638, SDNHM 87822; m2: SDNHM 105356; m3: SDNHM 39751, SDNHM 39752, SDNHM 55310, SDNHM 76983, SDNHM 39753; P3: SDNHM 105008; M1: SDNHM 31644, SDNHM 85697; M2: SDNHM 39757, SDNHM 39352, SDNHM 39755, SDNHM 46138; M3: SDNHM 96642, SDNHM 31642.

Horizon. Specimens range from lower, upper, and conglomerate tongues of the Friars Formation.

Specific diagnosis. As for genus.

Etymology. Named for Stephen L. Walsh, former SDNHM paleontologist, in recognition of his exceptional contributions to our understanding of the vertebrate paleontology and Eocene biostratigraphy of Southern California. Walsh collected and prepared many of the specimens described in this paper.

Description. The p3 of *Ekwiiyemakius* has smooth enamel and lacks exodaenodonty. The p3 also lacks a metaconid and exhibits no buccal nor anterobuccal cingulid. The p3 paraconid is cingulid-like and mesio-lingually positioned. The p3 talonid is mesiodistally long while the trigonid is mesiodistally short. Width of the p3 is very narrow; buccolingual width is less than half of mesio-distal length. There is a sharp cristid present on the distobuccal wall of the p3 protoconid. The p4 has a metaconid that forms a small distinct cusp that is slightly distolingually positioned relative to the protoconid. The mesiodistal length of the p4 is shorter than that of the m1. The p4 paraconid is a distinct, small cusp that is positioned lingually. The p4 paracristid is sharp, but the mesial portion is not elevated and the buccal protocristid is very distally oriented. The p4 has a lingual cingulid that is absent or weakly present, a weak mesiobuccal cingulid, and a strong buccal cingulid. The p4 hypoconid is heel-like and the entoconid is present as a small cusp. The p4 trigonid is proportionally shorter than the talonid, representing less than 40 percent of the total mesiodistal length. The lower molars of *Ekwiiyemakius* display well-developed buccal cingulids that are frequently discontinuous distally. The talonids of all lower molars are consistently wider than the trigonids. The m1 paraconid is a conical cusp that is positioned buccolingually between the protoconid and metaconid. The m1 metaconid is lower in height and very distolingually positioned compared to the

protoconid. The m1 trigonid is lingually open, and the paracristid is strong and long. The m1 entoconid is similar in size to the hypoconid. The m2 paraconid is a conical cusp that is is lingually positioned mesial to the metaconid but is not basally fused with the metaconid. The m2 metaconid is distolingually positioned relative to the protoconid, and the m2 trigonid is lingually open. The m2 entoconid is similar in size to that of the hypoconid. The m3 is mesiodistally longer than the m2. There is a single hypoconulid lobe on the m3 that is positioned near the midline. The upper molars of *Ekwiiyemakius* display a lingually discontinuous cingulum and a distinctly waisted distal margin. There is no post-protocone fold present on any of the upper molars. The M1 is smaller in size compared to the M2. The first and second upper molars have a well-developed conical hypocone that is distolingually positioned relative to the protocone. There is no pericone present on the M1, but a pericone is variably present on M2. The M1-2 paraconule and metaconule are distinct but small in size. The metacone on the M3 is much smaller in size compared to the paracone. The buccal cingula of M1-2 are strong, the distal and mesial cingula are weakly developed, and a lingual cingulum is intermittently present in the current sample. The M1-2 display a small but distinct parastyle and metastyle. The M1-2 also preserve a deep sulcus between the protocone and hypocone.

Discussion. *Ekwiiyemakius* most closely resembles *Omomys*. Shared features of *Ekwiiyemakius* and *Omomys* include relatively smooth dental enamel, lack of a postprotocone fold on upper molars, a waisted distal margin of M1-2, variable size of the hypocone on M1-2, and a variable presence of a pericone on the M2 (Cuozzo, 2008). *Omomys* and *Ekwiiyemakius* also share a p4 that has a well defined but small metaconid, a present mesiolingual cingulid, and a strong buccal and mesiobuccal cingulid. *Ekwiiyemakius* is distinguished from *Omomys* in being significantly smaller in overall size, as well as by having an M1 that lacks a pericone, has a discontinuous lingual

cingulum, and has larger conules (see Figure 22). *Ekwiiyemkaius* differs from *Omomys* in the presence of a sulcus between the protocone and hypocone on the M1-2. *Ekwiiyemakius* further differs from *Omomys* in having M1-2 with a more distinctly waisted distal edge, as well as the p3-4 lacking a lingual cingulid.

Order PRIMATES Linnaeus, 1758

Semiorder HAPLORHINI Pocock, 1918

Suborder OMOMYIFORMES Trouessart, 1879

Family OMOMYIDAE Trouessart, 1879

Subfamily OMOMYINAE Trouessart, 1879

CABRILLOTARSIUS, gen. nov.

Type species. *Cabrillotarsius randalli*

Generic diagnosis. Omomyine primate that differs from all other North American omomyiforms except *Omomys, Macrotarsius, Diablomomys, Chumashius, Rooneyia,* and *Ekwiiyemakius* in lacking a M1 post-protocone fold. Differs from all other omomyines in the P4 anterobuccal placement of the protocone. Length and width measurements of the upper and lower dentition are absolutely smaller than *Macrotarsius*, *Ourayia, Diablomomys*, and *Yaquius*. Measurements are absolutely larger than *Omomys*, *Utahia, Stockia,* and *Ekwiiyemakius* (see Table 3). Differs from *Omomys*, *Macrotarsius*, *Ourayi*a, *Diablomomys*, *Yaquius* and *Stockia* in having an m1 with a paraconid that is positioned mesial to the protoconid. Differs from *Omomys*, *Macrotarsius*, *Ourayia*, *Diablomomys*, *Stockia*, and *Utahia* in having m2-3 trigonid lingual cusps that are lower in height relative to the protoconid. Differs from *Omomys*, *Ekwiiyemakius*, *Stockia*, *Diablomomy*s, *Utahia* and *Macrotarsius* in having an m3 talonid that is similar in width relative to the trigonid. Differs from *Omomys*, *Utahia*, *Diablomomys*, and *Ekwiiyemakiu*s in lacking an m3

distobuccal cingulid. Differs from *Ekwiiyemakius*, *Diablomomys* and *Omomys* in having moderate levels of upper and lower molar occlusal surface crenulation. Differs from *Ekwiiyemakius*, *Macrotarsius*, and *Omomys* in having an M1-2 with a narrow stylar shelf. Differs from *Macrotarsius* and *Omomys* in having a P4 with a postprotocrista, and in having an M3 with a variably small or absent metacone. Differs from *Omomy*s in having more developed M1-2 hypocones, less developed pericones, and in having upper molars that are buccolingually broader in occlusal outline. Further differs from *Omomys* in lacking overlapping premolars, and in having a small P3 protocone and P4 parastyle. Differs from *Macrotarsiu*s in having an M1 with a waisted distal margin and in having m1-2 metaconids that are relatively smaller than the protoconid. Differs from *Washakius* in having weaker molar crenulations and having a lingually continuous cingulum.

Etymology. Named for the Spanish explorer, Juan Cabrillo, who led the first European expedition to what is now the west coast of the United States, including San Diego. In combination with *Tarsius*, in recognition of the probable stem haplorhine or stem tarsiiform phylogenetic affinities of the Omomyoidea.

CABRILLOTARSIUS RANDALLI, sp. nov. (Fig. 19)

Holotype. Specimen SDNHM 38126, partial right mandible with alveoli for i1-p2, and p3-m1 intact.

Paratypes. Specimen SDNHM 55250, partial left maxilla, with alveolus for P3, P4, M1, and M3 intact, and lingual half of the M2; SDNHM 46439, isolated P3; SDNHM 43094, isolated M2; SDNHM 56991, isolated m2; SDNHM 87871, isolated m3.

Hypodigm. Specimen SDNHM 31648, isolated P3; SDNHM 43097, SDNHM 38132, isolated P4s; SDNHM 38135, SDNHM 45826, SDNHM 60667, isolated M1s; SDNHM

37605, SDNHM 45826, isolated M2s; SDNHM 46560, isolated M3. SDNHM 58778, isolated p3; 55109, SDNHM 49270, partial mandible with m1 and m2 intact, SDNHM 60664, SDNHM 56990, SDNHM 85940, SDNHM 62283, SDNHM 51350, isolated m1s; SDNHM 55109, SDNHM 37600, SDNHM 60685, SDNHM 37599, SDNHM 60665, SDNHM 38129, isolated m2s; SDNHM 62224, SDNHM 56992, SDNHM 55445, SDNHM 37601, SDNHM 79804, SDNHM 85941, SDNHM 76982, SDNHM 40111, SDNHM 43814, isolated m3s.

Horizon. Specimens range from lower, upper, and conglomerate tongues of the Friars Formation.

Specific diagnosis. As for genus.

Etymology. Named for Kesler Randall, SDNHM fossil vertebrates collections manager, in recognition of his efforts to collect, prepare, and curate fossil mammals from San Diego County, and whose assistance with this project has been invaluable.

Description. The p3 of *Cabrillotarsius* is moderate in length, with the mesial-distal length longer than one half the length of the m1. The p3 protoconid is taller in height relative to that of the p4. The p3 buccal and mesiobuccal cingulids are weakly developed, and the p3 is lacking a lingual cingulid. The p3 paraconid is variable in form, being cingulid-like in some specimens, and forming a small, distinct cusp in others. The p3 hypoconid is present as a short heel without a fully developed cusp, and the entoconid is variably absent or present. The p4 of *Cabrillotarsius* has a mesiodistal length that is shorter than that of the m1. The p4 paraconid is absent, and the metaconid is present as a small distinct cusp. The p4 lingual cingulid is absent, while the mesiolingual cingulid is present weakly, and the buccal and mesiobuccal cingulids are strong. The p4 has a sharp ridge present on the distobuccal wall of the protoconid. The p4 hypoconid is present and heel-like while the entoconid is absent. The m1 paraconid is conical and is positioned mesial

to the protoconid. The m1 metaconid is lower in height relative to the protoconid and is positioned distolingually relative to the protoconid. The m1 trigonid is lingually open. The m1-2 buccal and mesiobuccal cingulids are strongly developed. The m2 of *Cabrillotarsius* has a conical paraconid that is positioned mesiolingually to the metaconid. The m2 trigonid is lingually closed. The m3 is longer in mesial distal length relative to the m1-2. The m3 talonid is similar in width to the trigonid. The m3 hypoconulid is variable in cusps present and position. The m2-3 show moderate trigonid mesiodistal compression. The m1-3 talonids are lingually closed by a low cristid. The P3 of *Cabrillotarsius* is smaller in size relative to the P4 or M1. The P3 paracone is taller in height relative to that of the P4. The P3 is lacking a metacone and has a small protocone. The P3 has a small parastyle, and is lacking a metastyle. The P3 has weak buccal and mesial cingula, is lacking a lingual cingulum, and has a strong distal cingulum. The P3 distal edge is waisted. The P4 of *Cabrillotarsius* is smaller in size relative to the M1. The P4 protocone is positioned anterobuccally, and the metacone and hypocone is lacking. The P4 has a parastyle and lacks a metastyle. The P4 buccal, distal, and mesial cingula are strong, but the lingual cingulum is absent. The P4 distal edge is waisted, this trait is variable for the mesial edge. The M1 is smaller in size relative to the M2. The M1-2 hypocone is small and positioned distolingually relative to the protocone. The M1 has a small paraconule and metaconule, and has weak pre- and postconule cristae. The M1 has a waisted distal edge. The M2 has a variably present pericone and post-protocone fold. The M2 distal edge is variably waisted. The M3 is small in size relative to the M1-2 and lacks a hypocone. The M1-3 have strong lingual cingula, and M1-2 have strong buccal cingula. The M1-2 have a small parastyle and metastyle, as well as a narrow stylar shelf. The M1-2 also have strong mesial and distal cingula. The upper and lower molar occlusal surfaces are slightly crenulated.

Discussion. *Cabrillotarsius* is most similar in morphology to *Omomys*, *Macrotarsius*, *Ourayia*, and *Brontomomys*. *Cabrillotarsius* and *Omomys* share an M2 with conical pericones and well-developed hypocones. *Ourayia, Macrotarsius* and *Cabrillotarsius* share crenulated enamel on upper and lower molar occlusal surfaces. The M1-3 of *Cabrillotarsius, Ourayia*, and *Macrotarsius* share well developed stylar shelves with strong buccal cingula. Intraspecific variation in the hypodigm of *Cabrillotarsius* includes the variable size of the M2 hypocone as well as the buccal half of the M2. The buccal portion of the M2 shows variation present in the stylar waisting of the upper molars. *Cabrillotarsius* differs from *Omomys*, *Macrotarsius*, and *Brontomomys* in having a P4 with an anterobuccally positioned protocone (see Figure 23), and in having a p4 postmetacristid. *Cabrillotarsius* differs from *Macrotarsius* and *Brontomomys* in being smaller in absolute size. Differ from *Omomys* and *Macrotarsius* in having an M3 with a variably absent or small metacone and having a strong, continuous lingual cingulum on M1 (Figure 23). Differs from *Macrotarsius* in having m1-2 metaconids that are relatively smaller than the protocone in size. *Cabrillotarsius* differs from *Omomys* in having M1-2 with more developed hypocone and less developed pericone. Further differs from *Omomys* in the upper molars being more buccolingually broad, the lower premolars lacking overlap, and the enamel occlusal surface having crenulation.

In 1980 Lillegraven published a comprehensive study on the Eocene primates of Southern California. In this work, Lillegraven included figures of multiple University of California Museum of Paleontology (UCMP) specimens from the Friars Formation of San Diego County, California (Lillegraven, p.186 and p.191, 1980), which were incorrectly attributed to *Omomys powayensis* [*Stockia powayensis*] according to Walsh (1996). It is relevant to *Cabrillotarsius* because after close examination of the photographs of the specimens in Lillegraven (1980), I believe the 16 teeth allocated to

Omomys powayensis likely belong to *Cabrillotarsius*. Similarities include size, strong lingual cingulum, M3 with a reduced metacone relative to paracone, lack of a post-protocone fold, and an M1 with a well-developed hypocone. The specimens from the UCMP are different from the holotype of *Stockia powayensis* in lacking heavily crenulated enamel on the molar occlusal surfaces and lacking any development of a lingual cingulid, which is present on the molars of *Stockia*. *Stockia* also differs from the UCMP specimens in having a more broad and deep talonids on the lower molars.

Order PRIMATES Linnaeus, 1758

Semiorder HAPLORHINI Pocock, 1918

Suborder OMOMYIFORMES Trouessart, 1879

Family OMOMYIDAE Trouessart, 1879

Subfamily OMOMYINAE Trouessart, 1879

BRONTOMOMYS, gen. nov.

Type species. *Brontomomys cerruti*

Generic diagnosis. Omomyine primate that differs from all other North American omomyiforms except *Omomys, Macrotarsius, Diablomomys, Chumashius, Rooneyia, Cabrillotarsius*, and *Ekwiiyemakius* in lacking a postprotocone fold on the upper first molar. Length and width measurements of the upper and lower dentition are absolutely smaller than *Macrotarius montanus*, and *Ourayia*, similar in size to *Macrotarsius jepseni* and *Mytonius*. *Brontomomys* is absolutely larger than *Omomys*, *Yaquius*, *Diablomomys*, *Stockia*, and *Utahia* (see Table 3). Differs from *Ekwiiyemakius*, *Cabrillotarsius*, *Yaquius*, *Stockia*, *Diablomomys*, *Utahia*, *Macrotarsius*, *Omomys*, and *Ourayia* in having an m2-3 paraconid that is positioned lingually and basally fused with the metaconid. Differs from *Ekwiiyemakius Yaquius*, *Stockia*, *Diablomomys*, *Macrotarsius*, *Omomys*, and *Ourayia* in

having m2-3 paraconids that are similar in size with the metaconid. Differs from *Ekwiiyemakius*, *Chumashius*, *Rooneyia*, *Diablomomys*, and *Omomys* in having molar occlusal surface crenulation, but differs from *Washakius, Stockia*, *Utahia*, and *Macrotarsius* in having less developed molar crenulation. The p4 differs from *Cabrillotarsius, Stockia, Macrotarsius, Omomys*, and *Ourayia* in having an entoconid that forms a small distinct cusp. Differs from *Diablomomys*, *Cabrillotarsius*, *Macrotarsius*, and *Omomys* in having a P3 that is similar in size relative to the P4. Differs from *Ekwiiyemakius*, *Cabrillotarisus*, *Diablomomys*, and *Omomys* in the M1 lacking a waisted distal edge, the M3 lacking a metaconule, and the M1-2 having a mesostyle. Differs from *Ekwiiyemakius, Diablomomys, Macrotarsius*, and *Omomys* in having M1-2 paracones that are taller in height relative to the protocone. Differs from *Yaquius, Macrotarsius*, and *Omomys* in the P4 lacking a metastyle. Differs from *Ekwiiyemakius, Cabrillotarsius*, and *Ourayia* in having a p3 with a lingual cingulid. Differs from *Cabrillotarsius, Macrotarsius*, and *Omomys* in lacking a p4 postmetacristid. Differs from *Yaquius, Macrotarsius*, and *Ourayia* in the presence of a mesiolingual cingulid on the p4. Differs from *Macrotarsius* and *Omomys* in the P3 lacking a metastyle and the M2 lacking a postparaconule and postmetaconule cristae. The P4 is lacking a waisted distal edge, which differs from *Cabrillotarsius* and *Omomys*. Differs from *Ekwiiyemakius* and *Macrotarsius* in having a p3 with a buccal cingulid. Differs from *Macrotarsius* and *Ourayia* in the small size of the p4 metaconid. Differs from *Cabrillotarsius* and *Macrotarsius* in having a weak m1 postmetacristid. Differs from *Washakius* in having a smaller paraconule and metaconule on M1-2. Differs from *Omomys* in lacking a metaconid on the lower p3. Differs from *Stockia* in having a p4 with a metaconid. Differs from *Ourayia* in having less quadrate occlusal outlines for the upper molars, and in lacking an M3 with a lingually continuous cingulum or metaconule. Differs from

Macrotarsius in lacking M1-3 connections between the mesostyle and the centrocristae, in having an M1 hypocone that is positioned distolingually relative to the protocone, and in lacking a p4 with an elevated mesial portion.

Etymology. From the Greek *brontē* ("thunder"), in reference to the large size of the genus, in combination with *Omomys*, type genus of the Omomyoidea.

BRONTOMOMYS CERUTTI, sp. nov. (Figs. 20-21)

Holotype. SDNHM 55253, mandibular fragment with p3-m3 and alveolus for p2, c, i1, i2

Paratypes. SDNHM 56700 maxillary fragment with M2-3; SDNHM 58008 isolated M1;

Hypodigm. SDNHM 55252 mandibular fragment with p3-m3 and alveolus for p2, c, i1, i2, SDNHM 60683, SDNHM 105007, SDNHM 60681, SDNHM 58005, SDNHM 55819, SDNHM 60684, SDNHM 60671

Horizon. Specimens range from lower, upper, and conglomerate tongues of the Friars Formation.

Specific diagnosis. As for genus.

Etymology. Named for Richard Cerutti, retired SDNHM paleontologist who collected many of the *Brontomomys* specimens described here, including the holotype.

Description. The p3 of *Brontomomys* is moderate in length, being greater than ½ the length of the m1. The p3 protoconid is taller in height relative to that of the p4 and m1. The p3 has a weak lingual, buccal and mesiobuccal cingulid. The paraconid on the p3 is variable. The p3 lacks a metaconid, has a small cusp hypoconid, and a variably sized entoconid. The p4 is shorter in mesiodistal length relative to that of the m1. The p4 protoconid is taller than that of the m1. The p4 paraconid is variable; in one specimen this cusp is absent, while another has a cingulid-like paraconid. The p4 metaconid is a small,

distinct cusp that is positioned slightly distolingually relative to the protoconid. The p4 lacks a lingual cingulid, and has a mesiolingual, buccal, and mesiobuccal cingulid. The p4 hypoconid and entoconid are small cusps. The lower premolar crowns of *Brontomomys* are slightly overlapping. The m1 paraconid is a conical cusp that is positioned mesiolingually to the metaconid. The m1 trigonid is lingually open. The m3 distal heel of *Brontomomys* is present and is shorter than the talonid proper. The m3 hypoconulid is positioned near the buccolingual midline. The m1-2 buccal and mesiobuccal cingulids are strong. The lower molars lack a lingual or mesiolingual cingulid. The m2-3 paraconids are positioned lingually and are basally fused to the metaconid. The m1-3 talonids are closed by a low cristid. The P3 of *Brontomomys* is moderate in size, being as large as the P4 but still smaller than the M1. The P3 paracone is taller in height relative to that of the P4. The P3-4 metacone and hypocone is absent and the protocone is present as a small cusp. P3-4 lack a metastyle but have a small cuspate parastyle. The P3-4 buccal, mesial, and distal cingula are all strong, while the lingual cingulum is absent. The P3 mesial and distal margins are waisted, but P4 lacks a similar waisting. The M1 is smaller in size relative to the M2. The M1-2 hypocone is present and positioned distolingually relative to the protocone. The presence of a pericone is variable on the M1 of *Brontomomys*; some specimens lack a pericone, while other specimens have a small, distinct cusp. The M1-2 paraconule and metaconule are small. The M1-2 lacks a waisted distal edge. The M1-2 buccal, mesial, and distal cingula are strong. The M1 has a continuous lingual cingulum, while on the M2 this trait is mesiolingually discontinuous. The M1-2 parastyle and metastyle are present as small cusps. The M1-2 have a narrow stylar shelf, and mesostyles.. The M2 lacks a pericone. The M3 is slightly smaller in size relative to that of the M1. The M3 hypocone is variable; in some specimens this feature is absent, in others the M3 hypocone is present

as a small cusp. The M3 has a weak post-protocone fold. The molars have a variable presence of a lingual cingulum. The upper and lower molar occlusion surface of *Brontomomys* is moderately crenulated.

Discussion. With dental dimensions similar to *Macrotarsius jepseni*, *Brontomomys* is noteworthy for its large size compared to most other omomyoids. *Brontomomys* is most similar in morphology to *Macrotarsius*, *Ourayia*, and *Cabrillotarsius*. All four taxa have p3 protoconids that are taller in height relative to the p4 or m1. They also share upper and lower molar occlusal surface crenulation. *Brontomomys* shares with *Macrotarsius* and *Ourayia* broad upper molars with a distinct stylar shelf, including a small mesostyle on the upper M1-2. The lower premolars of *Brontomomys*, *Macrotarsius*, and *Ourayia* show similarities in occlusal outline and level of cingulid development. *Brontomomys* differs from *Macrotarsius, Ourayia*, and *Cabrillotarsius* in having m2-3 paraconids that are lingually positioned and basally fused with the metaconid (see Figure 24), and in having a p4 with an entoconid present as a small cusp. Differs from *Macrotarsius* and *Ourayia* in having a p4 with a mesiolingual cingulid, and a p4 with a relatively smaller metaconid (see Figure 24). Differs from *Ourayia* and *Cabrillotarsius* in having a p3 with a lingual cingulid present. Differs from *Cabrillotarsius* in the M1 and P4 lacking a waisted distal edge. Differs from *Ourayia* in the M3 lacking a lingually continuous cingulum and a metaconule. *Brontomomys* differs from *Macrotarsius* in lacking M1-3 with a connection between the mesostyle and centrocristae.

Phylogenetic Analyses

The parsimony analysis of the Ni matrix produced a bootstrap 50% majority-rule consensus of 32 trees. Of the 510 total characters included in the Ni matrix, 181 characters are constant, 70 variable characters are parsimony-uninformative, leaving 259 parsimony-informative characters. The bootstrap majority-rule tree (Figure 14) shows *Cabrillotarsius* and *Brontomomys* as sister taxa. Basal to *Cabrillotarsius* and *Brontomomys* is *Yaquius*, followed by *Diablomomys*. These four taxa comprise the sister clade to *Stockia*, *Utahia*, and *Ourayia*. Basal to those seven taxa are *Ekgmowechashala* and *Macrotarsius*, respectively. *Ekwiiyemakius* is the sister taxon to this larger clade that includes *Cabrillotarsius*, *Brontomomys*, *Yaquius*, *Diablomomys*, *Stockia*, *Utahia*, *Ourayia*, *Ekgmowechashala*, and *Macrotarsius*. The bootstrap support values range from 7-98. Out of the omomyines, the only clades with > 50% bootstrap support are *Chumashius* + *Omomys*, and *Macrotarsius montanus* + *M. siegerti*.

The Bayesian analysis of the Ni matrix resulted in two runs of 3500000 generations with average standard deviation of split frequencies of 0.03. Run 1 resulted in 0.54 proportions of successful state exchanges between chains, run 2 resulted in 0.55. The majority-rule consensus tree (Figure 15) shows *Cabrillotarsius* and *Brontomomys* as sister taxa, with *Yaquius* and *Diablomomys* as the sister group to this clade. This clade of four is sister to a clade including *Stockia*, *Utahia*, *Ourayia*, and *Macrotarsius*. Basal to this group is *Ekwiiyemakius*.

The parsimony analysis of the Tornow matrix produced a bootstrap 50% majority-rule consensus of 11 trees. Of the 100 total characters included in the Tornow matrix, 1 character is constant, 7 variable characters are parsimony-uninformative, leaving 92 parsimony-informative characters. The bootstrap majority-rule tree (Figure

16) shows *Brontomomys* being the sister taxon to *Utahia,* with *Ourayia* basal to *Brontomomys,* and a clade containing *Ekwiiyemakius* and *Cabrillotarsius* basal to *Ourayia*. *Omomys*, *Macrotarsius*, and *Hemiacodon* are successive stem members of the clade that includes *Ekwiiyemakius, Cabrillotarsius*, and *Brontomomys*. The bootstrap values indicating node support are all below 50.

The Bayesian analysis of the Tornow matrix resulted in two runs of 2000000 generations with average standard deviation of split frequencies of 0.01. Run 1 resulted in 0.79 proportions of successful state exchanges between chains, run 2 resulted in 0.77. The majority-rule consensus tree (Figure 17) again shows *Brontomomys* as the sister taxon to *Utahia*. *Brontomomys* and *Utahia* in turn form a clade with *Ourayia* and *Omomys carteri*. *Cabrillotarsius* and *Ekwiiyemakius* are successive stem members of the clade that includes *Brontomomys, Utahia*, *Ourayia*, *Omomys, Macrotarsius, Hemiacodon, Washakius,* and *Shoshonius*.

DISCUSSION

Phylogenetics

The phylogenetic results produced four trees for comparison (Figs. 14 - 17). The Ni trees (Figs. 14 and 15) show *Cabrillotarsius* and *Brontomomys* as sister taxa in both analyses, with *Ekwiiyemakius* falling out further down the stem. Interestingly, the Tornow trees show *Brontomomys* as the sister taxa to *Utahia*, and *Cabrillotarsius* sitting basally down the tree with *Ekwiiyemakius*. In the Tornow parsimony tree (Figure 16), *Ekwiiyemakius* and *Cabrillotarsius* are equally basal, which is distinctively different in the Ni parsimony tree where *Cabrillotarsius* is further derived in its placement, relative to *Ekwiiyemakius*. One of the most apparent observations from the results of the phylogenetic analyses is that the four trees vary in the placement of the new San Diego taxa. The results of phylogenetic analyses vary according to (1) the choice of character-taxon matrix and (2) the use of parsimony versus Bayesian tree building methods.

The first source of variation is the underlying data matrix. Because the aim of this study is to understand the relationships of the new San Diego taxa to other known North American omomyoids, we initially started with the Tornow (2008) matrix, but also decided to include the Ni et al. (2016) matrix. The choice to also score the Ni et al. (2016) matrix was based upon the inclusion of European and Asian taxa, the greater number of dental characters included, and the more recent publication date. We only used the first 510 characters from the Ni et al. (2016) data matrix out of a total of 1890 as these characters related solely to dentition. Only the 35 omomyoid taxa + *Donrussellia* were selected from the 196 taxa present in the Ni et al. (2016). Because we sampled a relatively small section of a large character matrix, it is not too surprising that there are many invariable characters present throughout our small sample. This led to 218

characters being excluded from the Bayesian analysis, and 251 characters being excluded from the parsimony analysis.

The Tornow matrix was included because it was written especially for North American omomyoids, and includes some taxa not present in the Ni dataset. The North American omomyoid genera included in Tornow but not in Ni are: *Jemezius* and *Trogolemur*. The North American omomyoid genera in Ni and not included in Tornow are: *Yaquius*, *Stockia*, *Diablomomys*, *Chumashius*, *Dyseolemur*, *Rooneyia*, and *Strigorhysis*. There are 100 characters included in the Tornow (2008) matrix, 76 of which are dental. 1 character is constant, 7 variable characters are parsimony-uninformative, leading to 8 characters being excluded from the parsimony analysis, and one character excluded from the Bayesian analysis.

The second source of variation in the placement of the new San Diego taxa stems from the different tree-building methods used by the differing phylogenetic analyses. For many decades, parsimony methods have been the most widely used approaches for reconstructing phylogeny from standard phenotypic data (Wright and Hillis, 2014). One issue with parsimony analyses is that only parsimony-informative characters (which are only those characters that discriminate among varying tree topologies) are used in the analysis. The distribution of these parsimony-informative characters does not necessarily reflect the true distribution of all the observable characters, therefore creating a sampling bias (Wright and Hillis, 2014). This bias leads to poor estimates of character rate evolution and inflated estimates of character change. Lewis (2001) introduced versions of the Bayesian Mk model that correct for biases in character evolution. This likelihood method takes rate heterogeneity between sites into account, whereas the default for parsimony methods is for character change to be weighted equally (Wright and Hillis, 2014). Accounting for rate heterogeneity more accurately reflects evolutionary processes

as sampled characters within datasets usually evolve under differing rates, developmental processes, and modes of evolution (Clarke and Middleton, 2008; Wagner, 2012). The introduction of Bayesian analyses to morphology has powered a movement within paleontologists toward Bayesian analyses using the Mk model (Wright and Hillis, 2014).

A third source of variation was from multistate characters. The character states on the Tornow matrix are constructed in a way to minimize the need to score multiple character states for a given taxon. For example, Character 23 on the Tornow matrix is about the p4 anterobuccal cingulid development: (0) 100-91% absent, 0-9% broken distally; (1-9) frequency bins; (A) 9-0% absent, 91-100% broken distally; (B-L) frequency bins; (M) 9-0% broken distally; 91-100% complete (Tornow p.114, 2008). The Ni et al. matrix retains multistate characters, meaning it contains characters that are scored as (1, 0), with two or more states being present in the sample for that specific character. The main problem with multistate data relates to the means by which phylogenetic analyses address polymorphic character scores. PAUP* will import data with multistate characters with no errors. However, this software automatically analyses only the first value in the polymorphism and excludes additional character states (D. Cannatella, personal communication, March 23 2017). MrBayes will not load data sets that contain multistate characters. Possible solutions to this issue are to replace the multistate characters as missing data, or attempt to break down the polymorphic taxa into monomorphic subunits (Davis and Nixon, 1991), which then runs the risk of losing true interspecies variation. In our case, polymorphic characters were only an issue for the analyses using the Ni et al. (2016) data matrix, and they were replaced as missing data.

A fourth source of variation was tree instability, which stemmed from large amounts of missing data. The missing data stems partly from multistate characters being replaced as missing, but the majority of the missing data stems from the inherent

limitations of the fossil record. Some of the included taxa are known from a single specimen, like *Rooneyia*, or known from a small assortment of isolated teeth, as is the case with *Yaquius*. These poorly sampled omomyoid genera generate large gaps in our data, which leads to increased instability in tree topologies. Wright and Hillis (2014) investigated the effects of missing data on topological error and found that when there is no missing data, Bayesian-Mk results in lower error relative to parsimony analyses. They found that both Bayesian Mk and parsimony analyses perform poorly when there is missing data, although the negative effects of the missing data are much greater for parsimony than for the Bayesian analyses.

The fifth and final aspect to consider for explaining the tree topology variation in the present study is the overall number of characters in the analysis. The Ni matrix has almost three times as many characters included in the analyses compared to the Tornow matrix. Increasing the total number of characters in the analysis improves the performance for both Bayesian and parsimony analyses (Wright and Hillis, 2014).

Primate Richness during the Uintan

SOUTHERN CALIFORNIA

Primates have been recovered from four geologic units in Southern California, the Friars, Mission Valley, Santiago, and Sespe formations (Table 1 and Figure 1). Collectively, these early Cenozoic deposits span the earliest Uintan (Ui1) through the middle Arikareean (Lillegraven, 1980; Mason, 1990; Walsh, 1996). The published literatures states that there was a dramatic faunal shift between the early and late Uintan in Southern California (Golz and Lillegraven, 1977; Lillegraven, 1980; Walsh, 1991, 1996). Endemism in the early Uintan (Friars and Mission Valley Formations) of Southern

Califonia fauna has been considered low relative to the later Uintan because of the faunal similarities between the early Uintan fauna of California and Bridgerian faunas from Utah and western Wyoming (Lillegraven, 1980; Walsh, 1996). It is the later Uintan rocks of Southern California, mainly the Santiago and Sespe Formations, that have historically been considered to record higher levels of mammal endemism than the older, early Uintan formations (Golz and Lillegraven, 1977; Walsh, 1991, 1996). The evidence of this faunal shift is the presence of endemic Southern California primates such as *Dyseolemur*, *Chumashius*, and *Yaquius* in the Sespe and Santiago Formations. The cause of this increasing endemism during the Uintan has been cited as the result of major tectonic events along the Pacific coast of North America (Lillegraven, 1980).

The omomyine taxa presented here challenge the long-accepted notion that the Friars and Mission Valley Formations do not preserve an endemic fauna. The three new genera described here have only been identified from the Friars Formation of San Diego County, and may represent taxa that are endemic to Southern California. The regionalized nature of the new taxa indicates that endemism in the omomyoid fauna of the Friars Formation was established earlier than previously thought. It is interesting to note that other primates, mainly *Notharctus* and *Hemiacodon*, are known exclusively from pre-Uintan faunas in the western interior, while in Southern California they persist into the early Uintan (Golz and Lillegraven, 1977; Lillegraven, 1980; Walsh, 1996). It has been hypothesized that these later occurrences on the west coast in the early Uintan suggests that the southerly latitudes of coastal Southern California may have served as temporary climatic refugia for a variety of species that became extirpated earlier in geologic time in the western interior (Lillegraven, 1980).

NORTH AMERICA

Outside of Southern California, Uintan primates are known from deposits of the Washakie Formation in the Sand Wash Basin of Colorado and Wyoming, the Badwater and Tepee Trail locations in the Wind River Basin of Wyoming, the Owl Creek locality in the Absaroka Mountains of Wyoming, the Uinta Basin of Utah, the Trans-Pecos region of western Texas, and the Cypress Hills Formation in Saskatchewan (Williams and Kirk, 2008; Gunnell et al., 2009). Much of our understanding of middle Eocene primate richness in North America stems from patterns observed in the samples preserved in the Rocky Mountain interior basins, which is where primate fossils are found in greatest abundance. Bridgerian primates are best known from deposits in the Green River Basin, Bridger Basin, Wind River Basin, and Bighorn Basin of Wyoming. Uintan primates, on the other hand, are best known from the Uinta Basin of Utah, the Trans-Pecos region of west Texas, the Washakie Formation in southern Wyoming, and the San Diego and Ventura counties in California (Robinson et al., 2004; Williams and Kirk, 2008; Gunnell et al., 2009). *Omomys* has now been identified in the earliest Uintan Turtle Bluffs Member of the Bridger Formation (Kelly et al., 2015).

The addition of *Ekwiiyemakius*, *Cabrillotarsius*, and *Brontomomys* to the known North American omomyine diversity allows for a better understanding of primate richness in the Uintan. Previous workers, looking solely to the Rocky Mountain basins, interpreted primate richness to be declining through the Uintan (Gunnell and Bartels, 1999). Rasmussen et al. (1999:407) wrote, "one of several important faunal contrasts distinguishing the Uintan NALMA from the earlier Wasatchian and Bridgerian NALMAs is the great reduction in primate richness and the complete absence of the familiar, large bodied notharctines in the Rocky Mountain Region" (Gunnell and Bartels, 1999). This interpretation of primate decline stems from more than 20 Bridgerian primate taxa named

from the southern Green River Basin that virtually disappear by the Uintan (Williams and Kirk, 2008).

More recent work shows that while primate richness declines in the greater Green River Basin during the Uintan, primate richness increases during the Uintan in other locations in North America (Westgate, 1988; Walsh, 1996; Kirk and Williams, 2008; Williams and Kirk, 2008; Gunnell et al., 2009; Kelly et al., 2015). It is now understood that adapiform richness and anaptomorphine richness severely decline during the Uintan. *Trogolemur* is the only member of the anaptomorphines to persist past the Bridgerian. On the other end of the spectrum, omomyine richness remained relatively stable through the Middle Eocene. Williams and Kirk (2008) wrote that the Bridgerian records fourteen omomyines species and the Uintan records fifteen. The work presented here increases the number of Uintan omomyines known from fifteen to eighteen. The recent work in Southern California, Utah, and West Texas illustrates the importance of looking beyond the Rocky Mountain interior for a better understanding of North American primate richness during the middle Eocene.

CONCLUSIONS

The three new genera of middle Eocene primate from the Friars Formation of San Diego County, California represent three new omomyine taxa. *Ekwiiyemakius*, *Cabrillotarsius*, and *Brontomomys* form a clade with the omomyine primates *Utahia*, *Ourayia*, *Omomys*, and *Macrotarsius*. The three new taxa may also be close relatives to *Yaquius*, *Diablomomys*, *Chumashius*, and *Stockia*. Phylogenetic tree topology varies due to underlying character matrix, analyses used, amount of missing data, and variance in number of characters. The scope of this project is not to fix all of the issues surrounding omomyoid systematics, but to gain a better understanding of evolutionary relationships in lower latitude Uintan omomyines.

Friars Fm.	Mission Valley Fm.	Santiago Fm.	Sespe Fm.
?*Omomys* sp.		*Dyseolemur pacificus*	*Dyseolemur pacificus*
Hemiacodon sp.			*Chumashius balchi*
Ourayia sp.	*Ourayia* sp.		*Yaquius travisi*
?*Macrotarsius* sp.	?*Macrotarsius* sp.		
Washakius woodringi	*Washakius woodringi*		
Stockia powayensis			

Table 1: Previously known omomyine primates from Middle Eocene formations of Southern California. Compiled from Lillegraven (1980), Mason (1990), and Walsh (1991, 1996).

Taxa	m1 area (mm^2)	All primate regression (g)	Prosimian regression (g)
Ekwiiyemakius	3.7	**131** (124 – 138)	**119** (113 – 125)
Cabrillotarsius	6.4	**348** (330 – 366)	**289** (275 – 303)
Brontomomys	11.6	**1008** (958 – 1061)	**757** (719 – 796)

Table 2: Estimated body mass of fossil taxa based on m1 area. All estimates calculated using least-squares regression formulae presented in Conroy (1987). Estimated body mass (bold) and 95% confidence range (pararentheses are expressed in grams. m1 area is the product of maximum mesiodistal length by maximum buccolingual width of the crown area.

Taxa	Average length of the m1 (mm)	Average width of the m1 (mm)
Ekwiiyemakius walshi	2.13	1.76
Cabrillotarsius randalli	2.75	2.33
Brontomomys cerutti	3.98	2.92
Macrotarsius montanus	4.45	3.95
Macrotarsius seigerti	4.32	3.61
Macrotarsius jepseni	3.96	3.27
Ourayia uintensis	4.19	3.34
Mytonius hopsoni	3.73	3.25
Utahia kayi	1.83	1.47
Yaquius travisi	4.30	3.80
Omomys carteri	2.49	1.98
Washakius woodringi	1.96	1.59
Dyseolemur pacificus	2.01	1.76
Stockia powayensis	2.83	2.11

Table 3: Average length and width measurements of Uintan omomyines (mm). The m1 of the new taxa described here and previously published Uintan omomyine taxa for comparison. Measurements of previously published taxa are from the Paleobiology Database (Behrensmeyer and Turner, 2015).

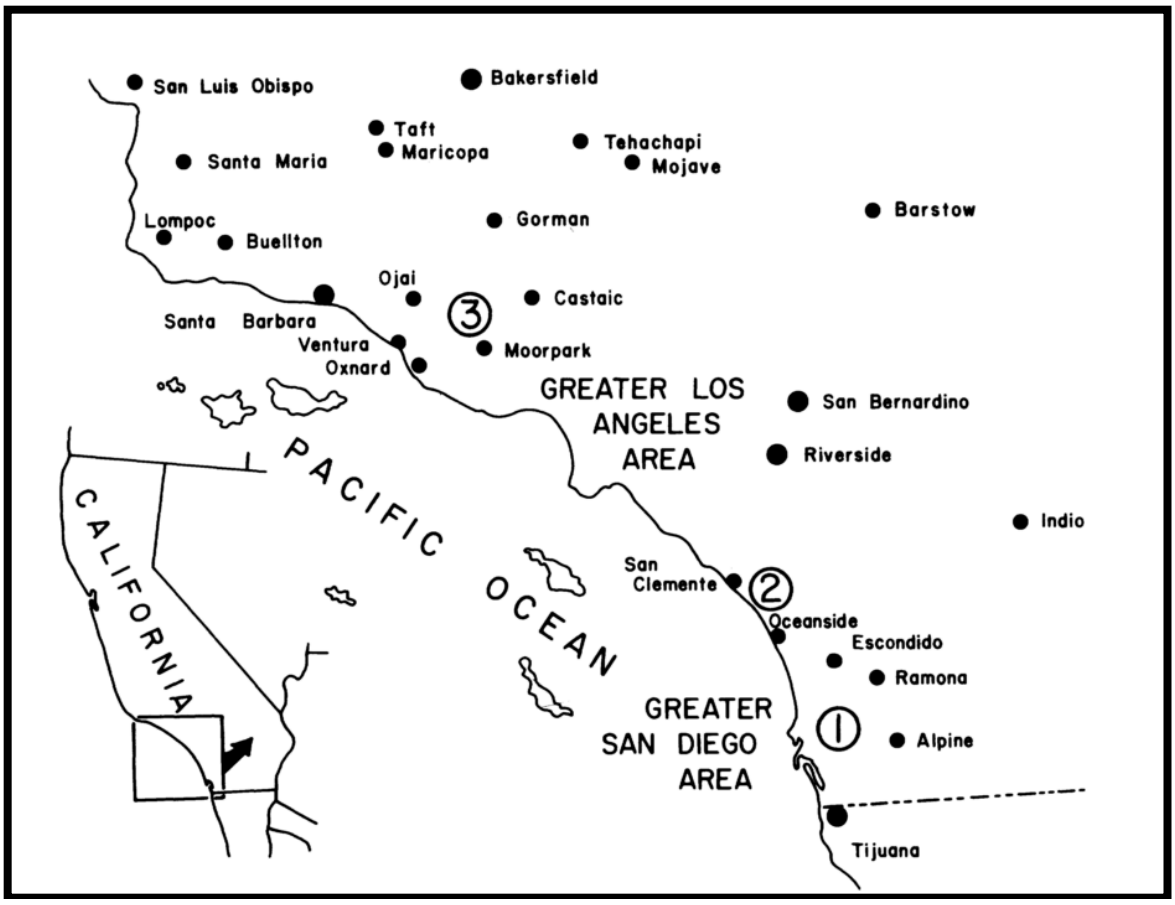

Figure 1: Reference map of the Uintan outcrops of Southern California. 1, greater San Diego area (Friars and Mission Valley formations); 2, San Clemente-Oceanside area (Santiago Formation); and 3, Ventura Co. (Sespe Formation). From Lillegraven (1980).

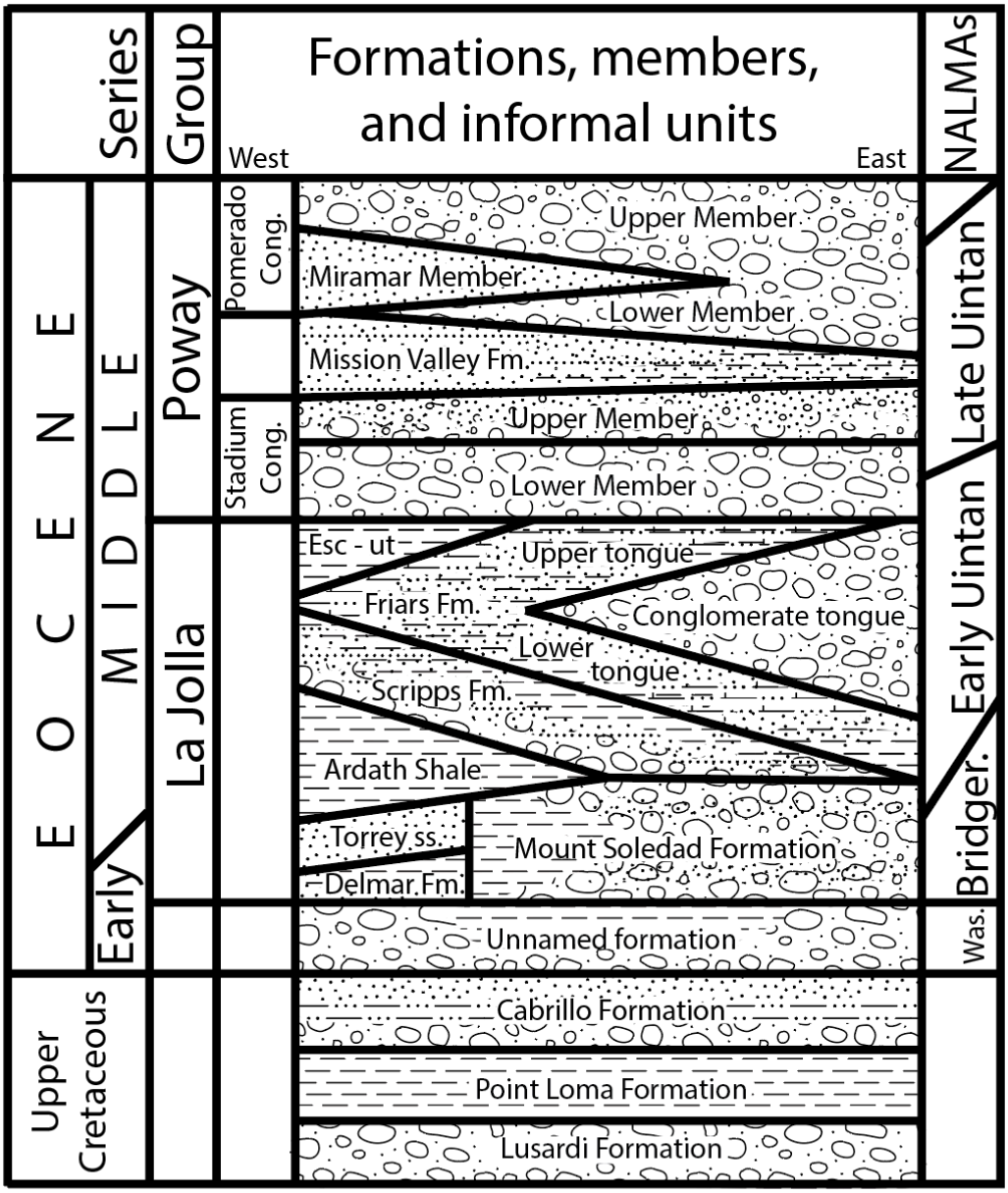

Figure 2: Stratigraphy of San Diego County. Modified from Walsh (1996).

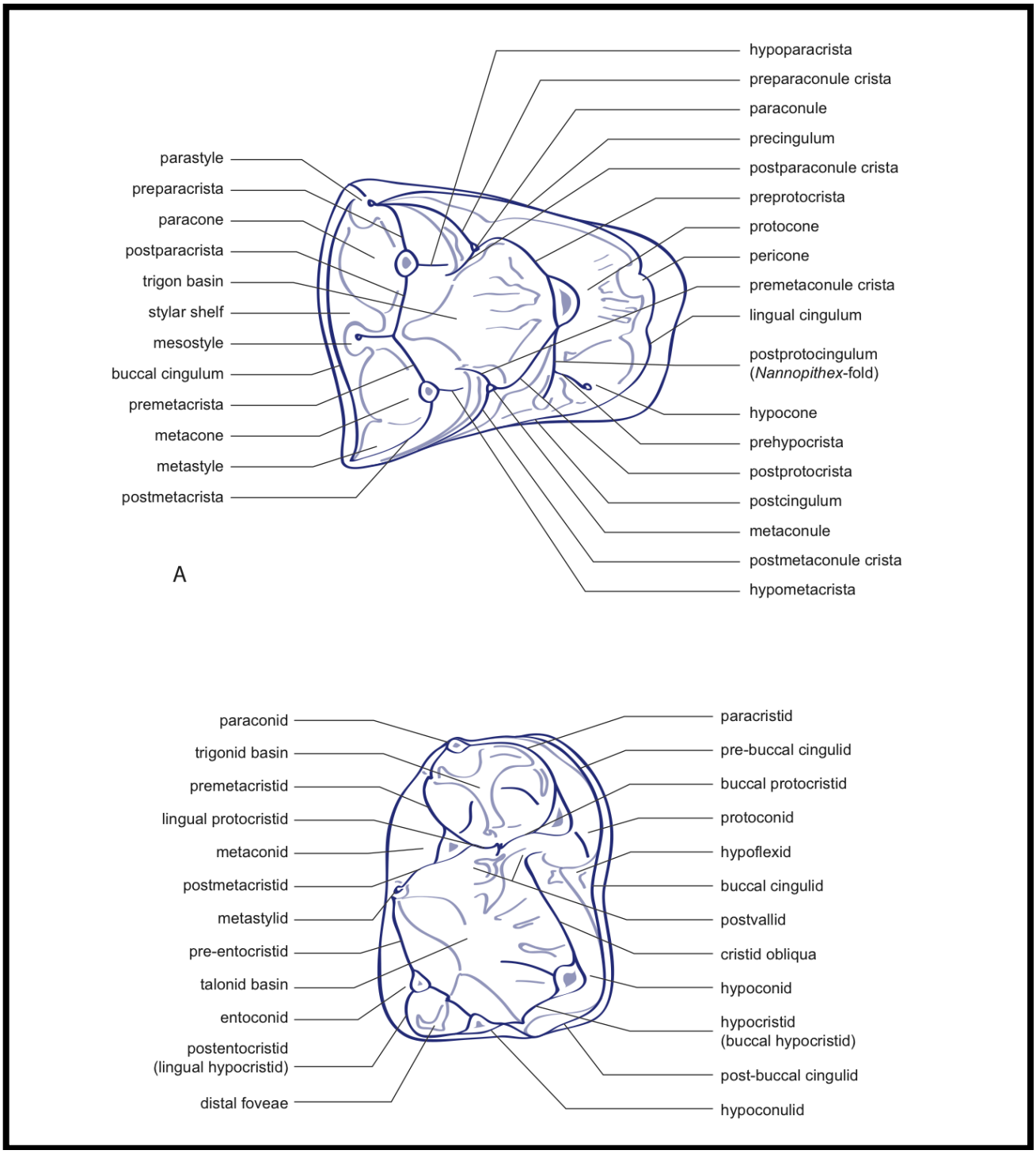

Figure 3: Nomenclature. Follows that of Ni et al. (2016).

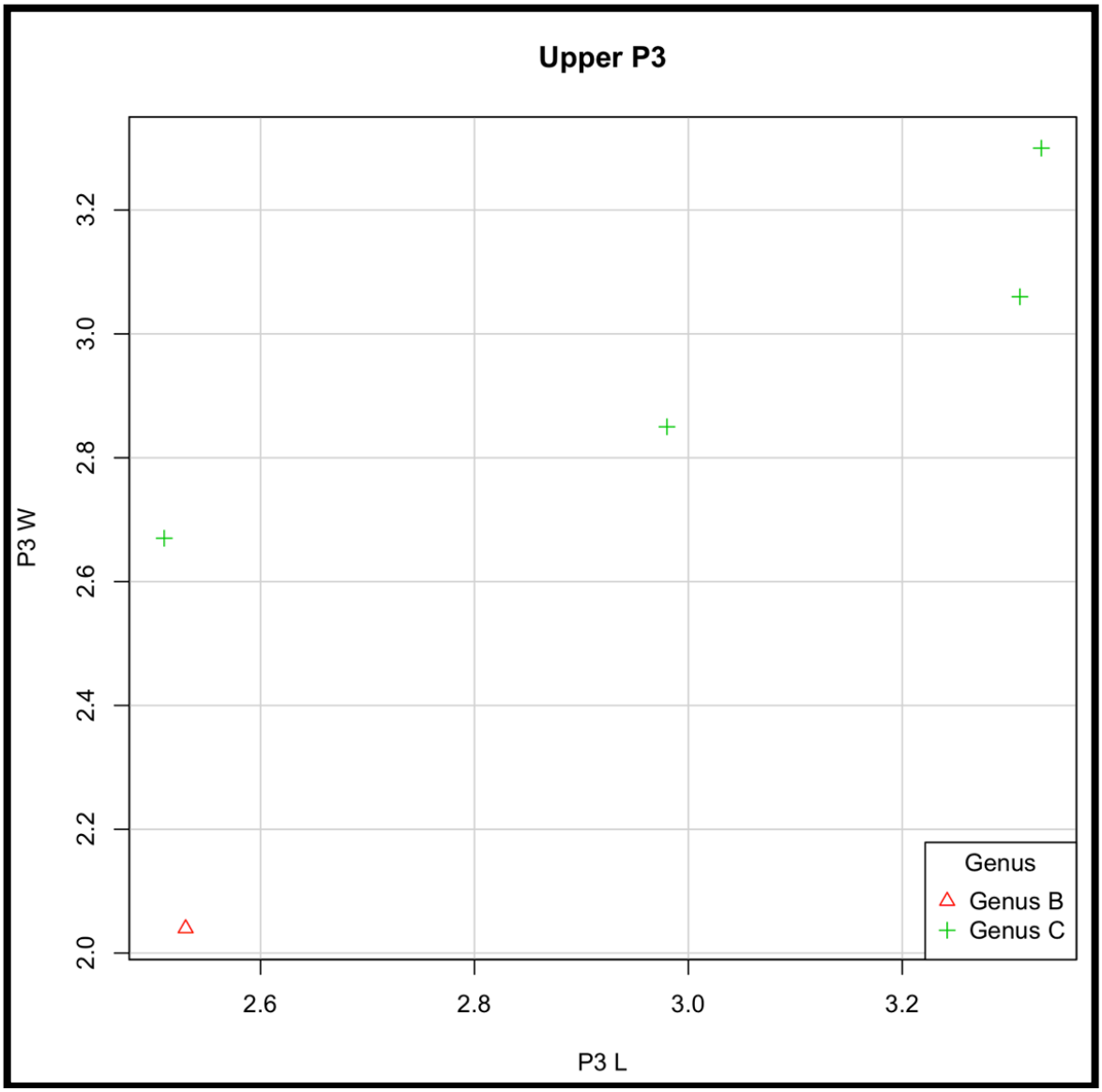

Figure 4. P3 Length x Width (mm). Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

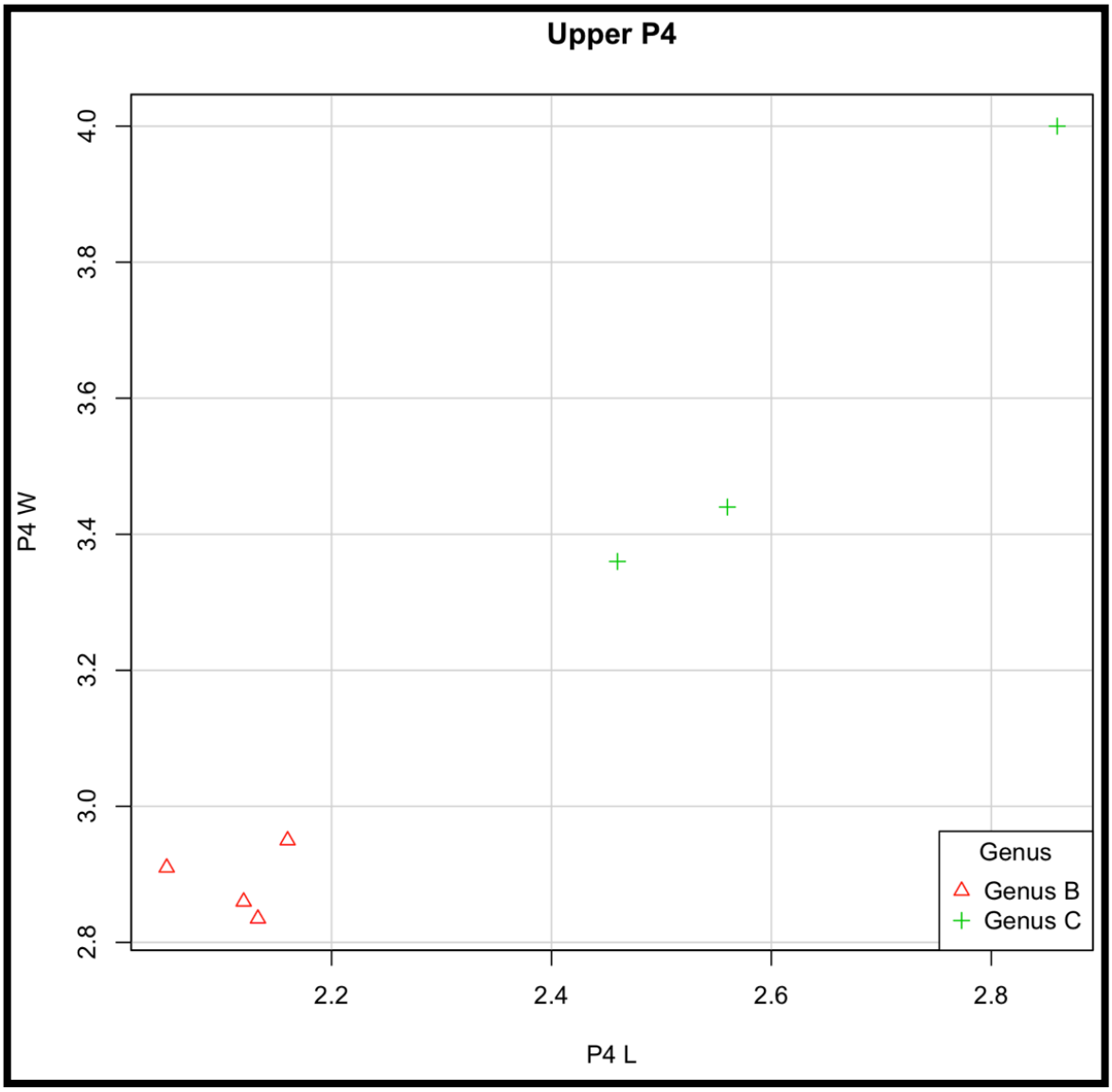

Figure 5. P4 Length x Width (mm). Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

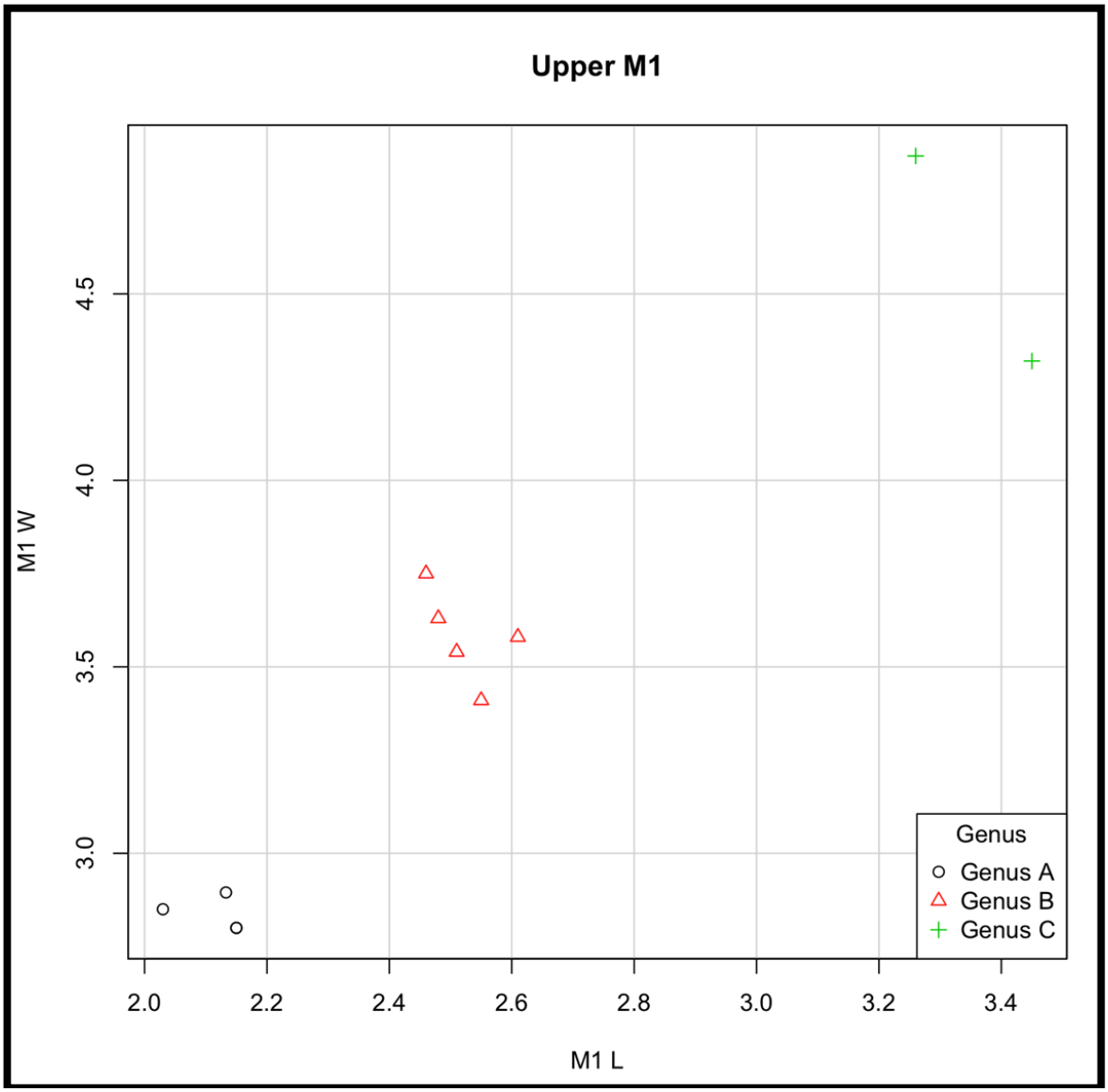

Figure 6. M1 Length x Width (mm). Genus A = *Ekwiiyemkius*; Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

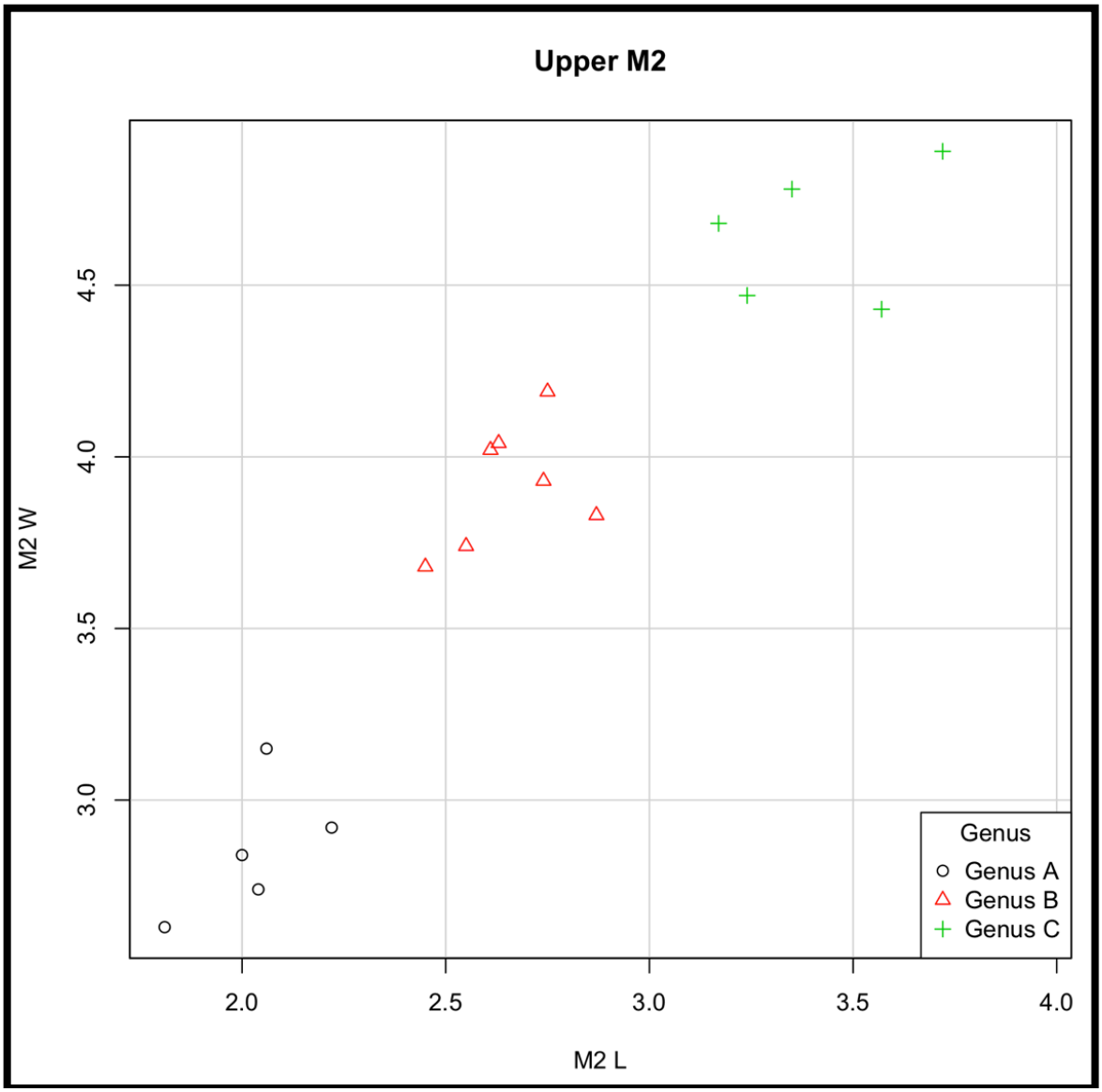

Figure 7. M2 Length x Width (mm). Genus A = *Ekwiiyemkius*; Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

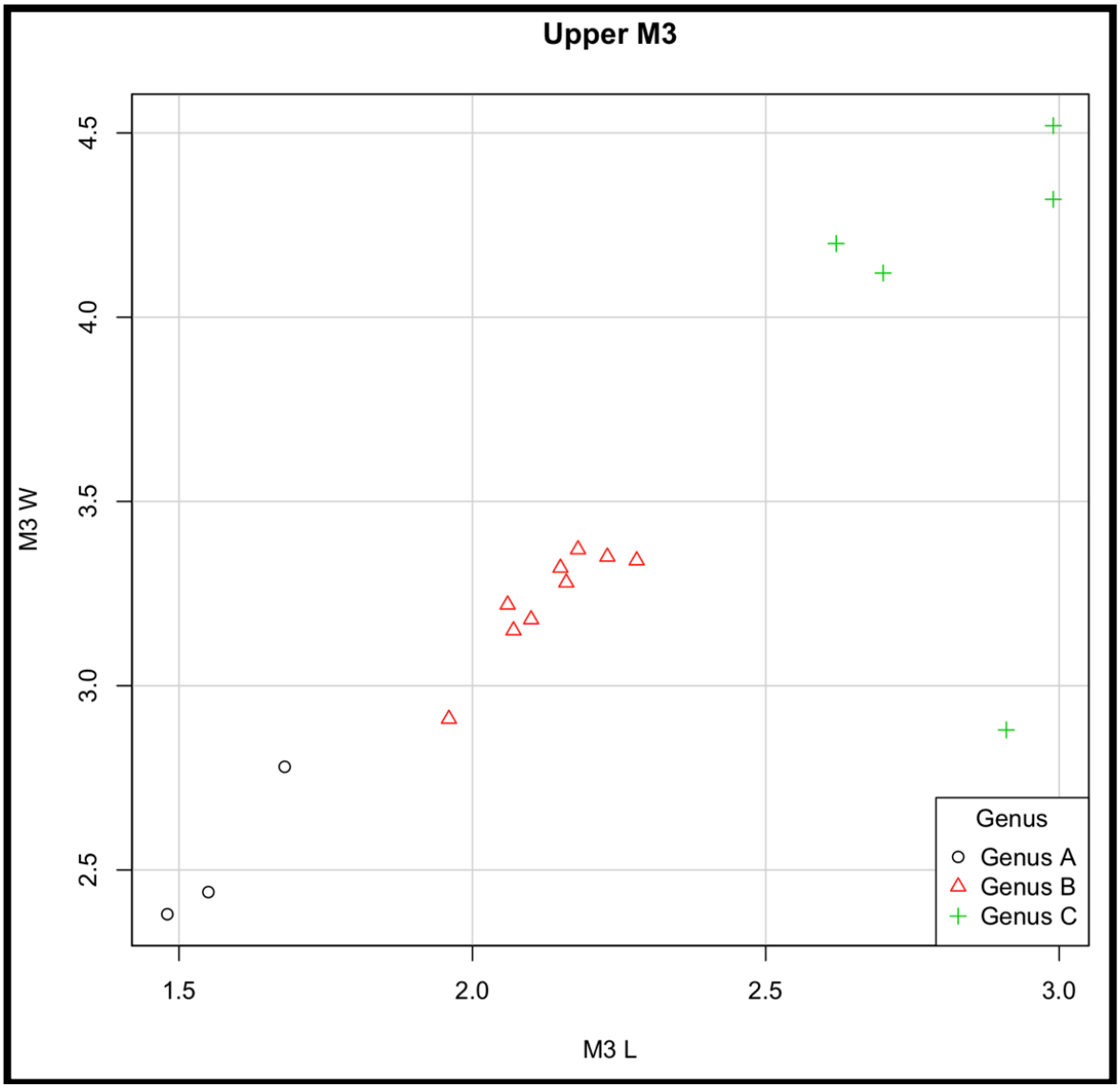

Figure 8. M3 Length x Width (mm). Genus A = *Ekwiiyemkius*; Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

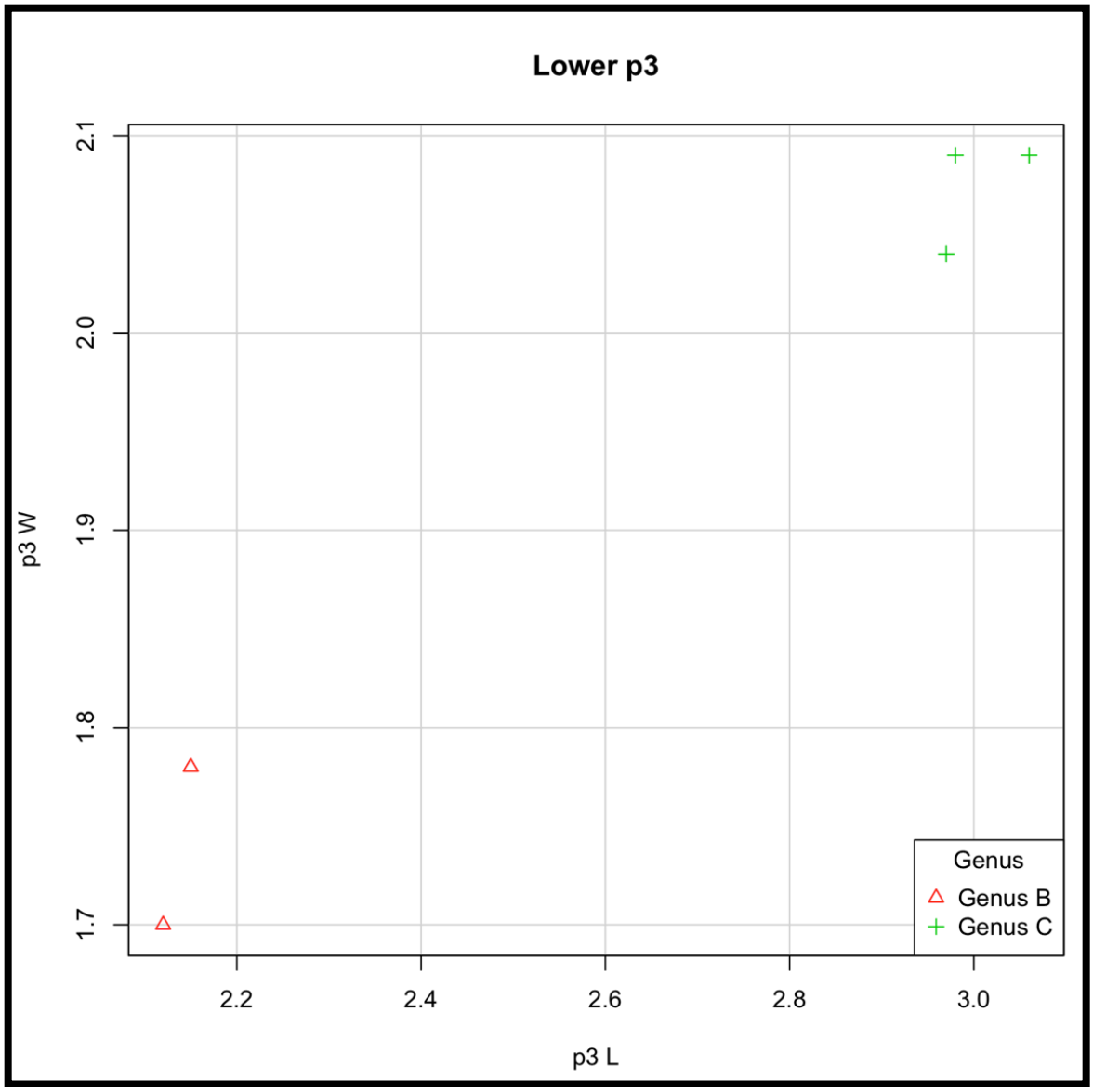

Figure 9. p3 Length x Width (mm). Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

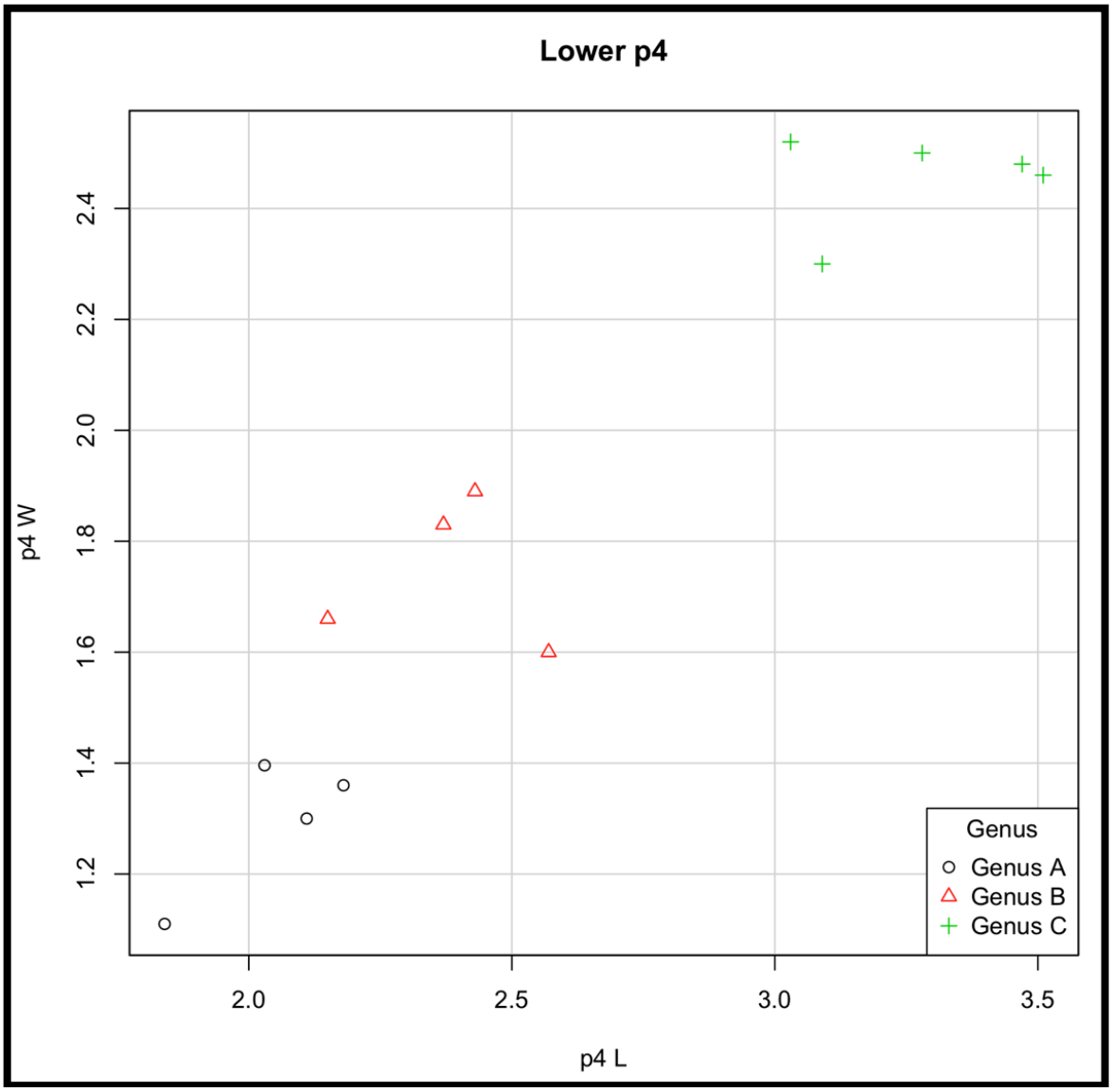

Figure 10. p4 Length x Width (mm). Genus A = *Ekwiiyemkius*; Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

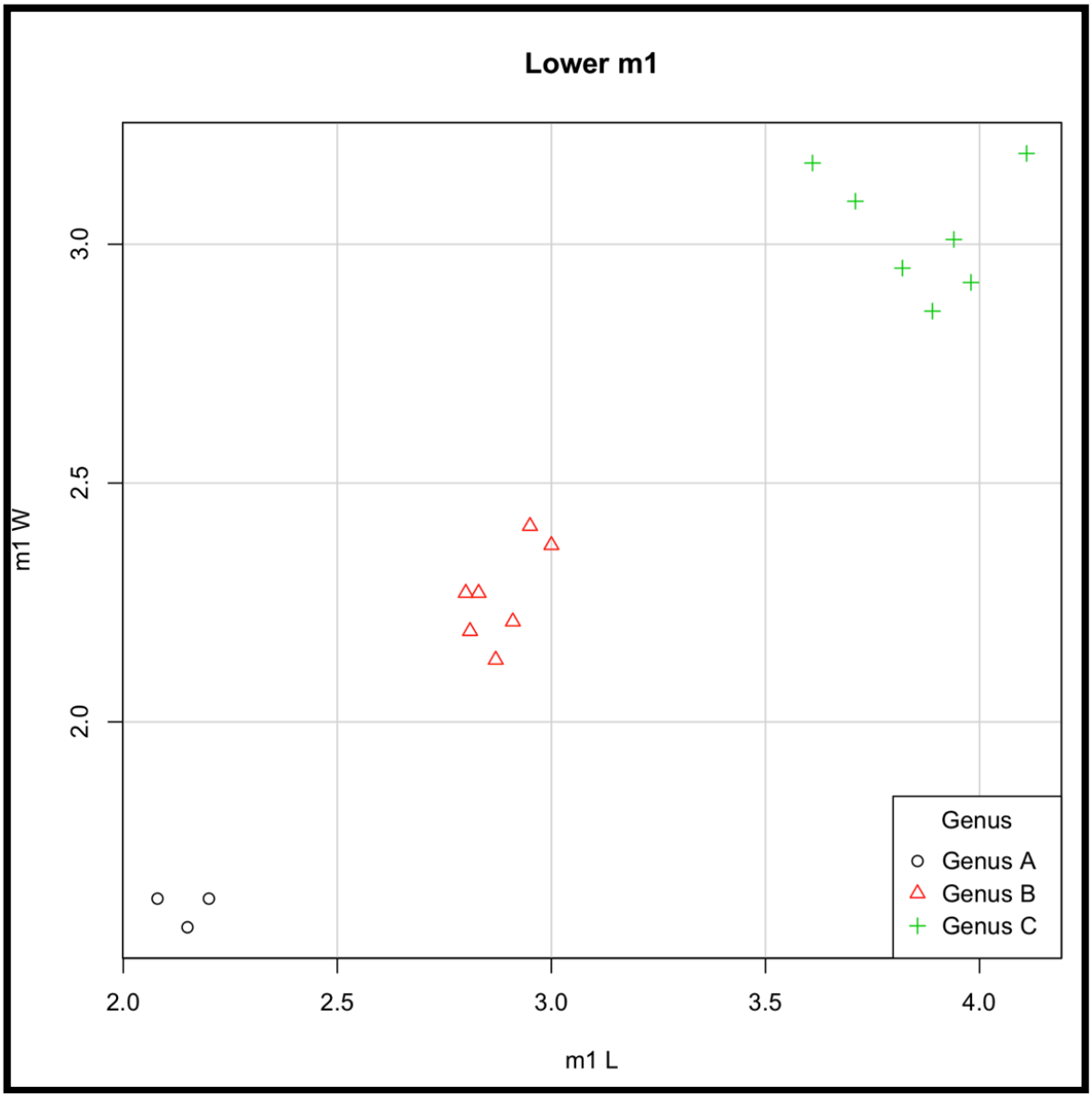

Figure 11. m1 Length x Width (mm). Genus A = *Ekwiiyemkius*; Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

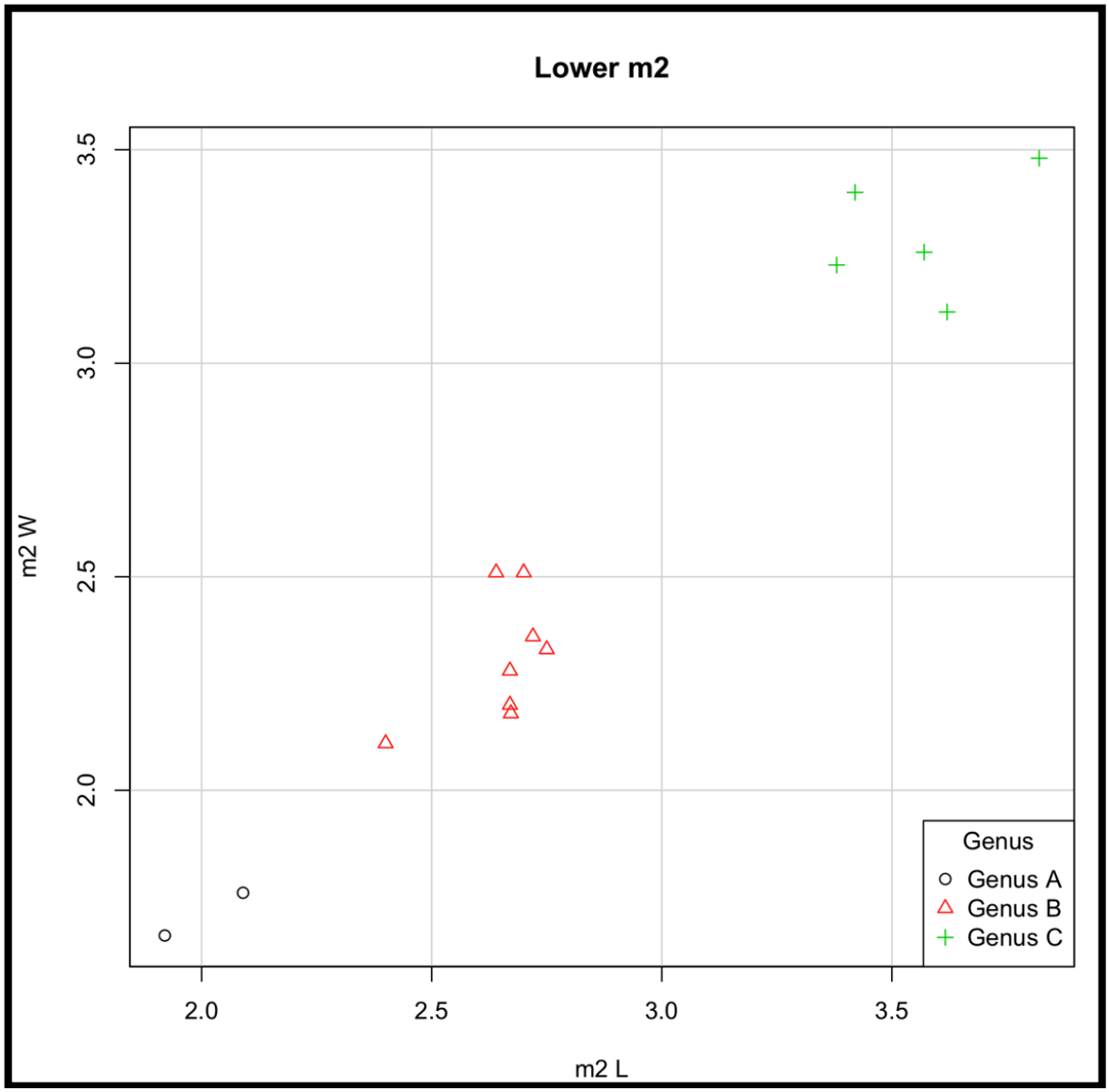

Figure 12. m2 Length x Width (mm). Genus A = *Ekwiiyemkius*; Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

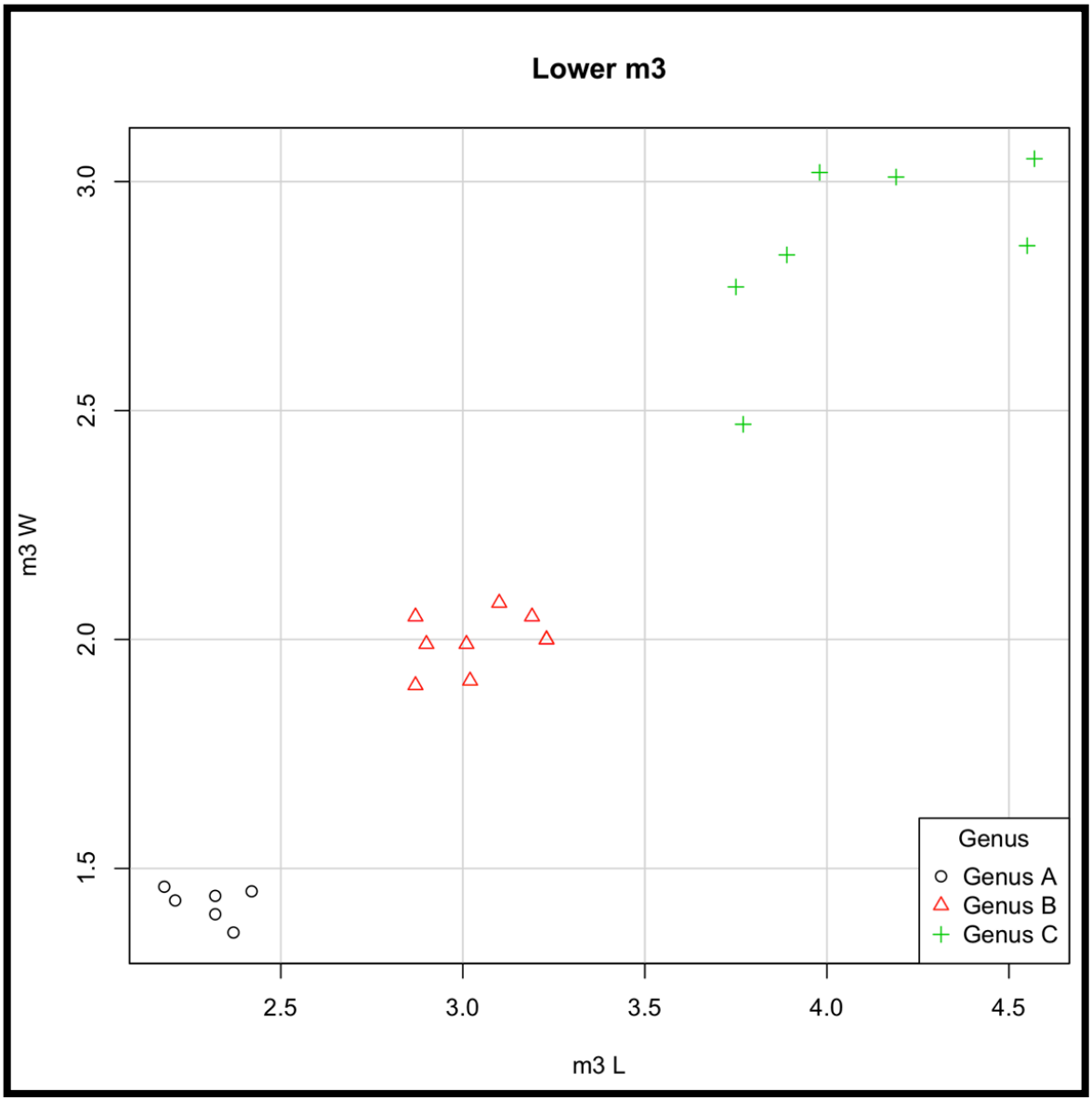

Figure 13. m2 Length x Width (mm). Genus A = *Ekwiiyemkius*; Genus B = *Cabrillotarsius*; Genus C = *Brontomomys*

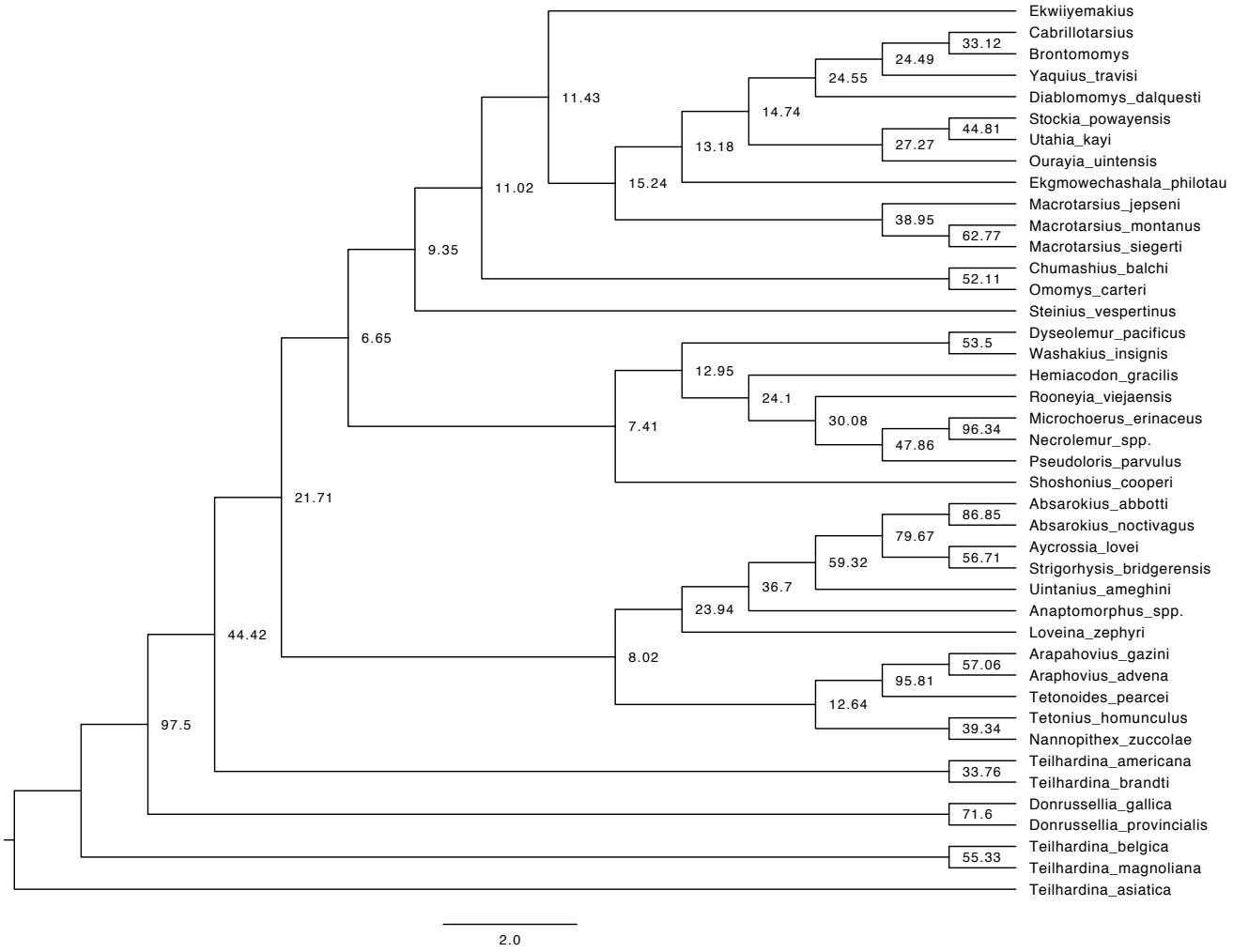

Figure 14. Ni Parsimony Results. Phylogenetic Majority-Rule tree produced through parsimony analysis using PAUP* and the Ni et al. (2016) character taxon matrix, plus addition of new taxa. Values at nodes represent bootstrap support.

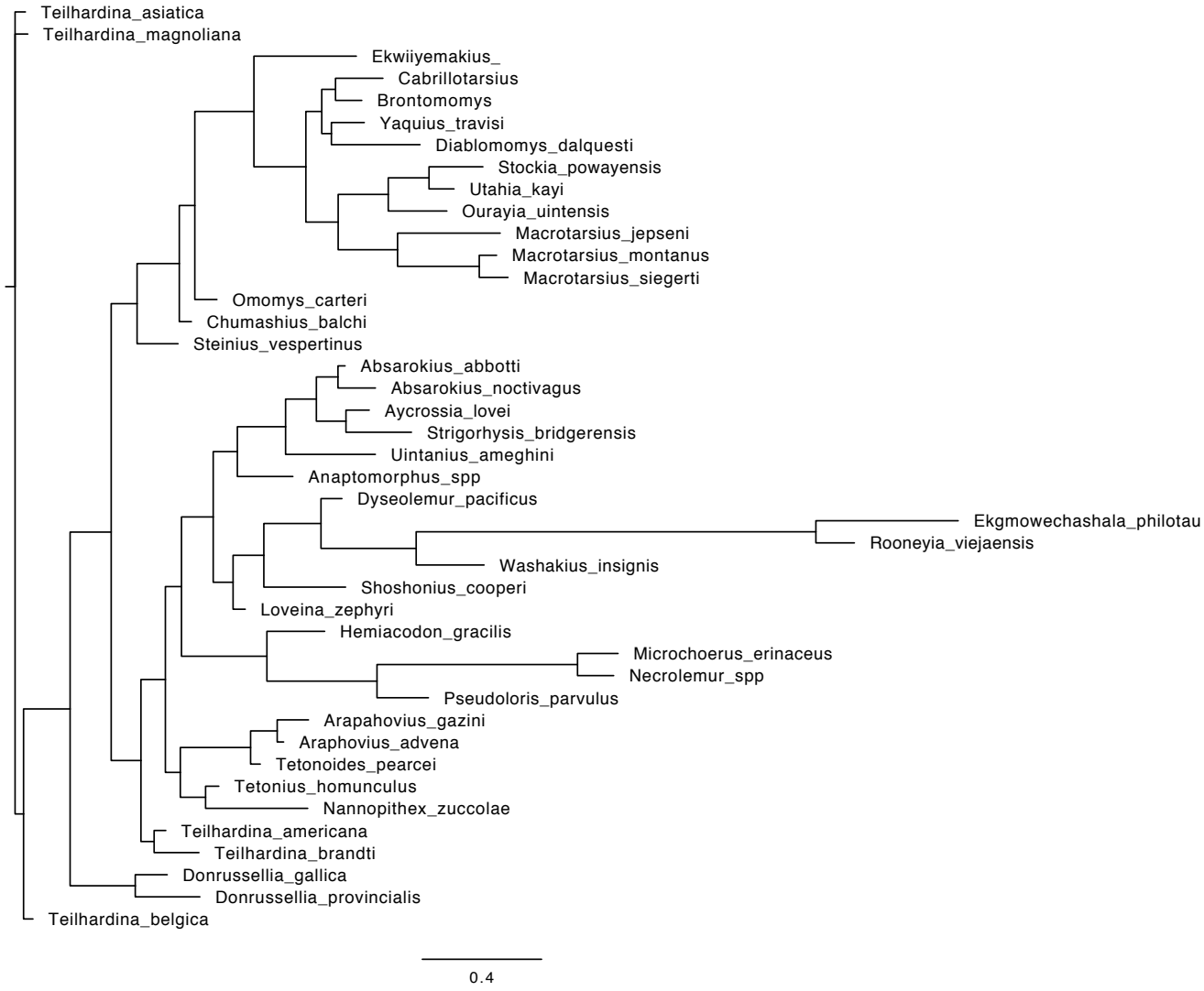

Figure 15. Ni Bayesian Results. Phylogenetic Majority-Rule tree produced through Bayesian analysis using MrBayes and the Ni et al. (2016) character taxon matrix, plus addition of new taxa described here.

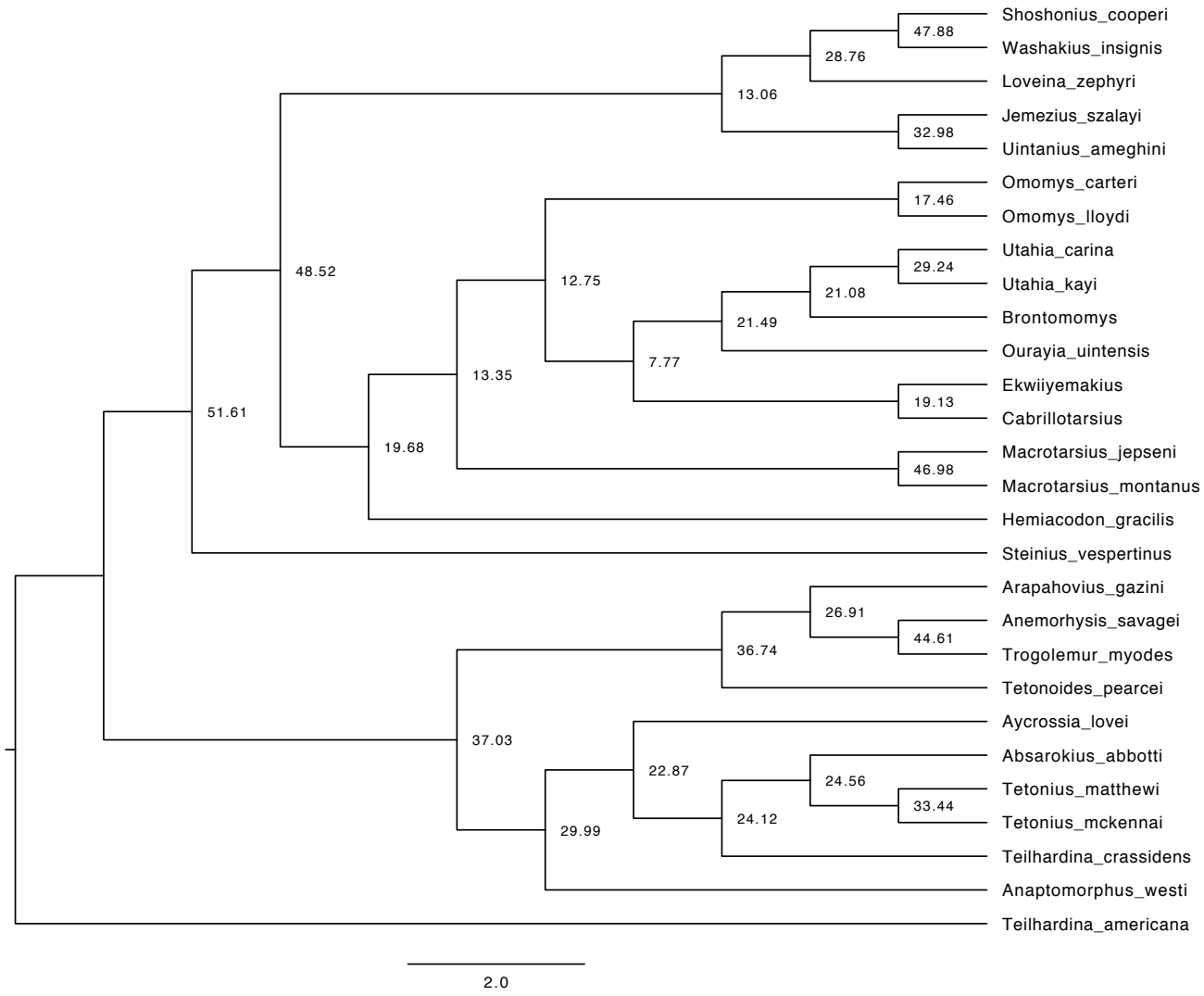

Figure 16. Tornow Parsimony Results. Phylogenetic Majority-Rule tree produced through parsimony analysis using PAUP* and the Tornow (2008) character taxon matrix, plus addition of new taxa. Values at nodes represent bootstrap support.

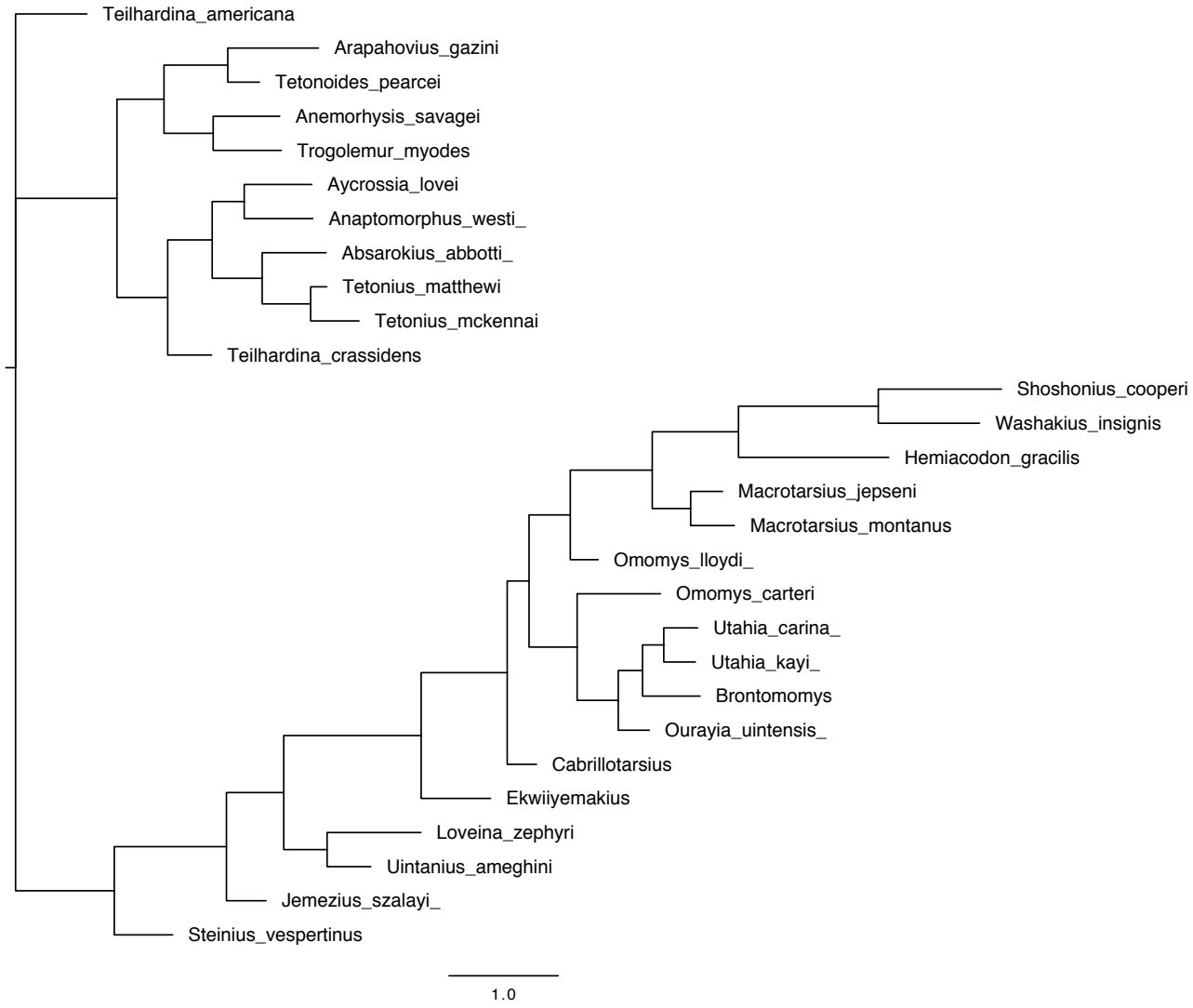

Figure 17. Tornow Bayesian Results. Phylogenetic Majority-Rule tree produced through Bayesian analysis using MrBayes and the Ni et al. (2016) character taxon matrix, plus addition of new taxa described here.

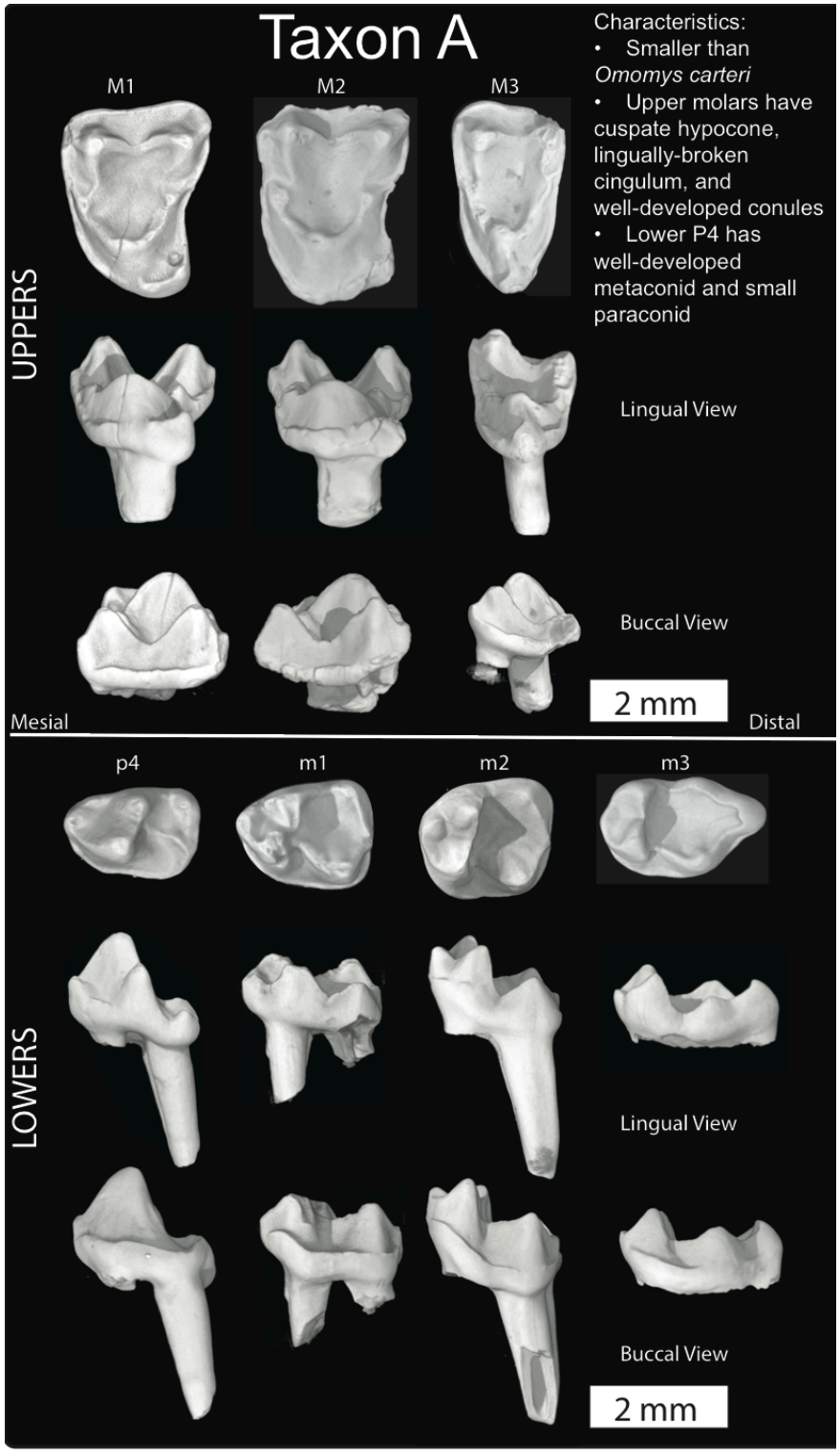

Figure 18: Upper and lower dentition of *Ekwiiyemakius walshi*.

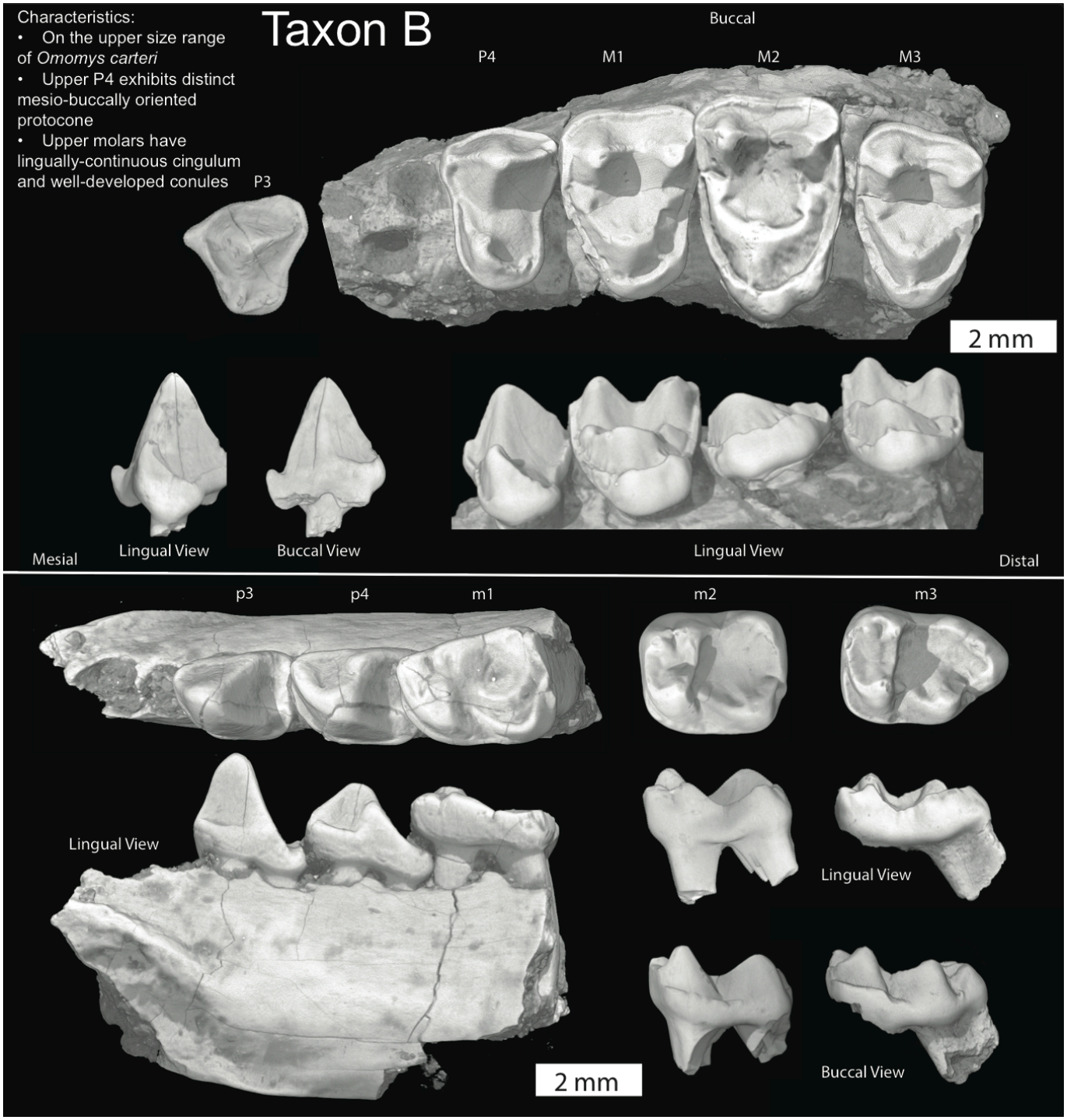

Figure 19: Upper and lower dentition of *Cabrillotarsius randalli*.

Figure 20: Upper and lower dentition of *Brontomomys cerutti*. Top photo: the holotype for *Brontomomys*, SDNHM 55253, occlusal view, p3-m3 present. Lower photo: occlusal view of SDNHM 56700 M2-3.

Figure 21: Side views of *Brontomomys* mandible. Holotype mandible fragment of *Brontomomys cerutti,* SDNHM 55253, with p3-m3 preserved. Upper photo: buccal view of lower dentition; Lower photo: lingual view of lower dentition.

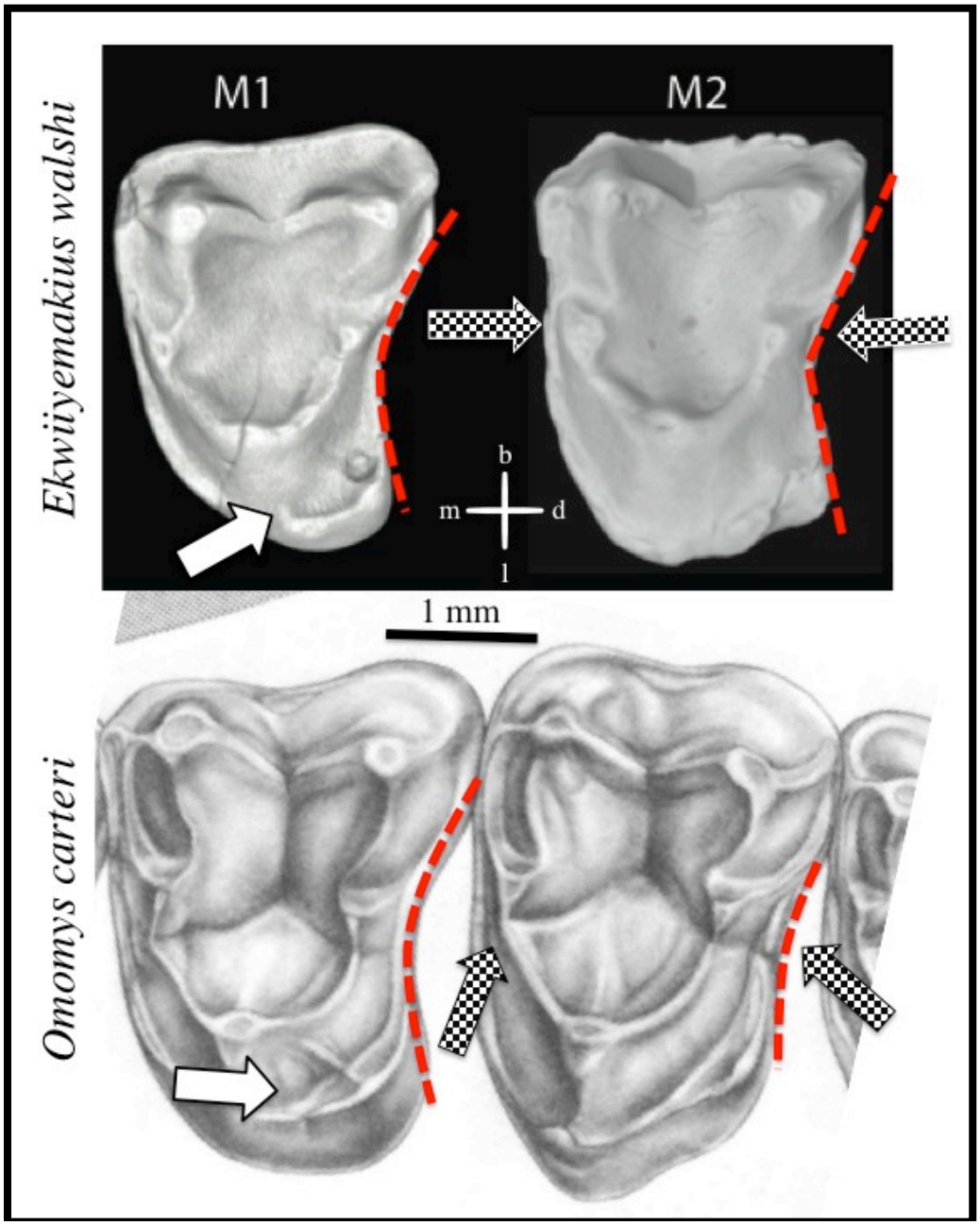

Figure 22. *Ekwiiyemakius* comparisons. The M1-2 of *Ekwiiyemakius* compared to *Omomys carteri*. *Ekwiiyemkaius* differs from *Omomys* in the presence of a sulcus between the protocone and hypocone on the M1-2 (white arrow), *Ekwiiyemakius* has relatively larger conules (checkered arrows), and *Ekwiiyemakius* further differs from *Omomys* in having M1-2 with a more distinctly waisted distal edge (dashed red line). Drawings are from Szalay (1976).

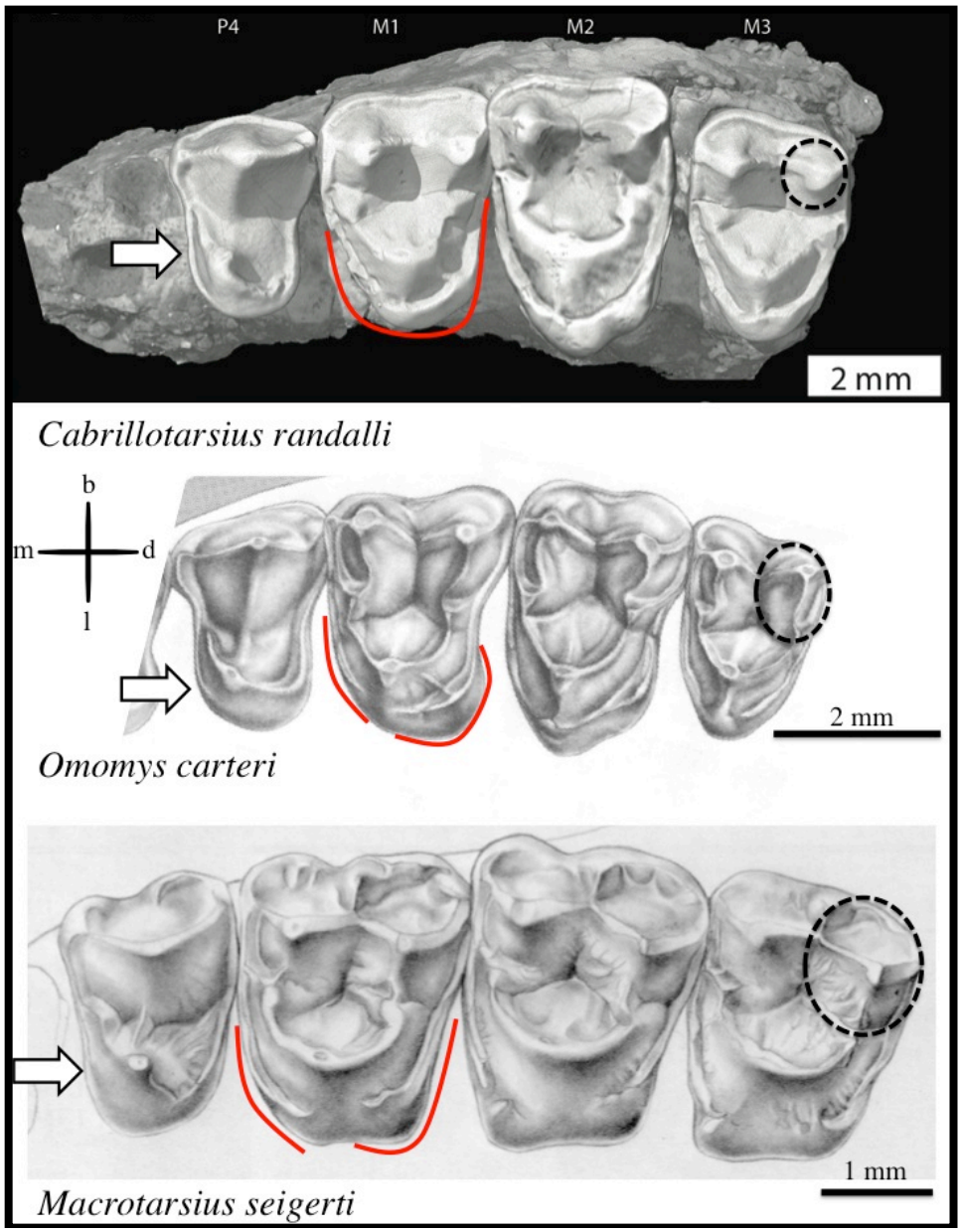

Figure 23: *Cabrillotarisus* comparisons. The P4 – M3 of *Cabrillotarsius* compared to *Omomys carteri* and *Marcrotarsius seigerti*. *Cabrillotarsius* differs from *Omomys* and *Macrotarsius* in having a P4 with an anterobuccally positioned protocone (white arrow). Further differs from *Omomys* and *Macrotarsius* in having an M3 with a variably absent or small metacone (dashed line) and in having a strong, continuous lingual cingulum on M1 (solid red line). Drawings are from Szalay (1976).

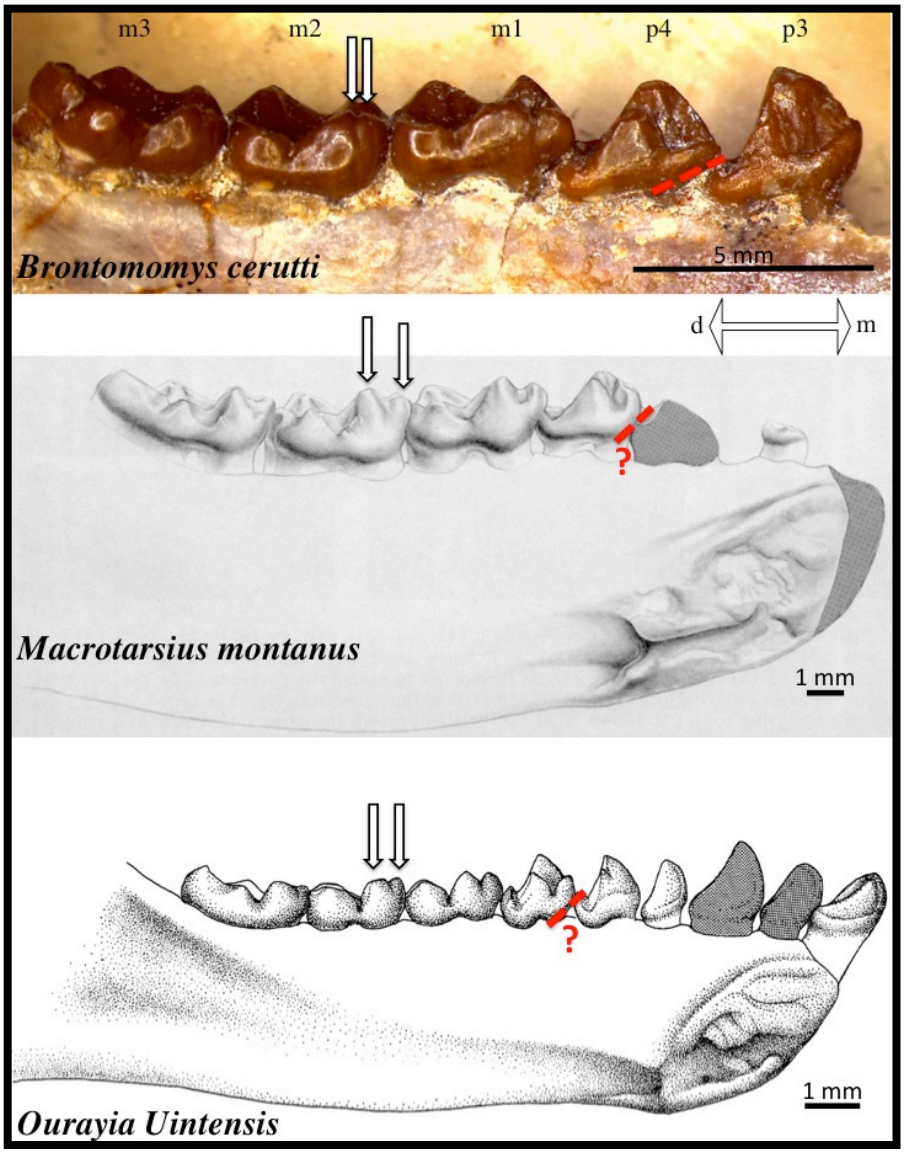

Figure 24. *Brontomomys* comparisons. The holotype of *Brontomomys cerutti*, SDNHM 55253, compared to *Macrotarsius montanus* and *Ourayia uintensis*. *Brontomomys* differs from *Macrotarsius* and *Ourayia* in having m2-3 paraconids positioned basally and lingually fused with the metaconid (white arrows), and in having a mesiolingual cingulid present on the p4 (dashed red line). Drawings are from Szalay (1976).

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Vita

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